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NATURAL HISTORY OF TURRITELLINE GASTROPODS (CERITHIODEA: TURRITELLIDAE): A STATUS REPORT

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ABSTRACT

A new review of available information, published and unpublished, on the biology and paleobiology of turritelline gastropods expands our knowledge of this important group, which is among the most abundant and widespread marine gastropod clades of the past 130 million years. It also highlights many areas in which additional research is needed.

Living turritellines are mainly sessile, semi-infaunal suspension feeders, in shallow waters of full-marine salinity and temperatures below 20°C, but they can occasionally be more active and diverse in their habits, crawling on the surface and thriving in a variety of depths, salinities, and temperatures. They are eaten by a surprising diversity of predators, and infected by numerous parasites, especially trematodes, but little is known about interactions with predators, parasites, competitors, or commensals in nature. Their reproductive patterns (broadcast spawning and spermatophores) appear to depend on high abundance, which may help explain why they are the dominant species in many marine communities. The larvae of most species float (or swim) and feed in the plankton for no more than 2 weeks, but nothing is known about settlement. Several fossils and at least one modern species are brooders. Spermatozoa are dimorphic, and frequently paired and/or multiflagellate.

Soft anatomy is known for only a few species, and ranges of variation remain largely undocumented. Radulae in particular have been strangely neglected, and this paper presents only the second published SEM image of a turritelline radula. Shell growth rates are variable but can be relatively rapid. Most species appear to live less than three years. Little is known about shell function or development. Although there is strong evidence for a positive correlation of abundance with available nutrients and/or primary productivity, this has not been examined quantitatively or experimentally.

Gathering such natural history information on marine gastropod groups should be as high a priority as systematic and phylogenetic analyses. Information scattered in the literature is now much more available via internet search tools, and this approach should be used for other groups.

Key words: predation, spermatozoa, reproduction, radulae, feeding, parasites.

> "*Perhaps the strongest argument in support of natural history is simply the magnitude of our current ignorance about nature. …*"
>
> (Wilcove & Eisner, 2000)

INTRODUCTION

The current crisis in systematics has been frequently noted (Winston, 1992; Feldmann & Manning, 1992; Savage, 1995; Wilson, 2004; Agnarsson & Kuntner, 2007; Wheeler, 2010): there are not enough systematists to describe and interpret the diversity of life that is rapidly disappearing. Less widely appreciated is the equally dire need for documentation of natural history – the basic biology of species. Although it is frequently seen as old-fashioned and far from cutting-edge science by both the public and many scientists, natural history is still the crucial basis for almost all organismal (and much sub-organismal) biology, from systematics and behavior to ecology and genetics. Many fundamental biological questions and pressing societal problems – from evolution to natural product prospecting to conservation – cannot be addressed without more and better basic natural history information (Bartholomew, 1986; Greene, 1986, 2005; Futuyma, 1998; Grant, 2000; Wilcove & Eisner, 2000; Dayton, 2003).

In this context, turritelline gastropods (Family Turritellidae, subfamily Turritellinae, mostly *sensu* Marwick, 1957a, b; Table 1) are certainly among those groups that deserve detailed documentation of their natural history. Turritelline shells are not large and showy (as are, e.g., members of Volutidae or Faciolariidae), nor are they of great economic importance (e.g., Strombidae or Haliotidae); they are neither among the most diverse marine gastropod groups (e.g., Turridae or Conidae), nor the subject of intense ecological study (e.g., Littorinidae). Yet turritellines are among the most important gastropod groups of the past 130 million years. Paleontologically, they are one of the most abundant, geographically widespread,

TABLE 1. Generic and subgeneric names that have been used for living and fossil species in the family Turritellidae. Subfamily classification modified slightly from Marwick (1957a, b).

Taxon	Authority	Age
Subfamily Turritellinae		
Acutospira	Kotaka, 1959	Eocene
Amplicolpus	Marwick, 1971b	Paleocene-Miocene
Archimediella	Sacco, 1895	Oligocene
Bactrospira	Cossmann, 1912	Pliocene
Callostracum	Smith, 1909	Recent
Calvertella	Petuch, 1988	Miocene
Coeloconica	Eames, 1957	Eocene
Colposigma	Finlay & Marwick, 1937	Paleocene
Colpospira	Donald, 1900	Eocene-Recent
Colpospirella	Powell, 1951	Recent
Costacolpus	Marwick, 1966	Late Cretaceous
Cristispira	Allison, 1965	Eocene
Ctenocolpus	Iredale, 1924	Miocene-Recent
Eurytorus	Gardner, 1947	Miocene
Gazameda	Iredale, 1924	Miocene-Recent
Hataiella	Kotaka, 1959	Oligocene-Miocene
Haustator	Montfort, 1810	Eocene-Recent
Idaella	Kotaka, 1959	Miocene
Kapalmerella	Allmon, 2005	Paleocene-Eocene
Kurosioia	Kotaka, 1959	Pleistocene
Leptocolpus	Finlay & Marwick, 1937	Paleocene
Maoricolpus	Finlay, 1926	Oligocene-Recent
Mariacolpus	Petuch, 1988	Miocene
Neohaustator	Ida, 1952	Pliocene-Recent
Nipponocolpus	Kotaka, 1959	Recent
Peyrotia	Cossmann, 1912	Miocene
Platycolpus	Donald, 1900	Recent
Reymentella	Adegoke, 1977	Paleocene
Sechuritella	Olsson, 1944	Late Cretaceous
Spirocolpus	Finlay, 1926	Eocene

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Taxon	Authority	Age
Springvaleia	Rutsch, 1942	Miocene
Stiracolpus	Finlay, 1926	Pliocene-Recent
Torcula	Gray, 1847	Eocene-Recent
Torculoidella	Sacco, 1895	Pliocene
Torquesia	Douvillé, 1929	Cretaceous-Eocene
Tropicolpus	Marwick, 1931	Oligocene
Turritella	Lamarck, 1799	Cretaceous-Recent
Vermicularia	Lamarck, 1799	Pliocene-Recent
Wyatella	Adegoke, 1977	Eocene
Zeacolpus	Finlay, 1926	Pliocene-Recent
Subfamily Protominae		
Protoma	Baird, 1870	Miocene-Recent
Protomella	Thiele, 1931	Recent
Subfamily Pareorinae		
Craginia	Stephenson, 1952	Late Cretaceous
Mesalia	Gray, 1847	Paleocene-Recent
Motyris	Eames, 1952	Eocene
Pareora	Marwick, 1931	Oligocene
Sigmesalia	Finlay & Marwick, 1937	Eocene
Tachyrinchella	Titova, 1994	Oligocene
Tachyrhynchus	Mörch, 1868	Recent
Woodsalia	Olsson, 1929	Eocene
Zaria	Gray, 1847	Recent
Subfamily Turritellopsinae		
Glyptozaria	Iredale, 1924	Recent
Kimberia	Cotton & Woods, 1935	Recent
Orectospira	Dall, 1925	Recent
Turritellopsis	Sars, 1878	Recent

and recognizable marine macrofossil groups of the Cretaceous and Cenozoic: they occur as fossils on every continent and in almost all marine deposits since the Early Cretaceous, and are frequently the dominant or even the sole macrofossil in assemblages in which they occur (reviewed in Allmon, 1988, 2007). This rich fossil record reveals that at least some turritelline species evolve rapidly compared with many other gastropods (Kauffman, 1972, 1977). For all of these reasons, turritellines are among the most biostratigraphically useful molluscan groups for this time interval (Woodring, 1930, 1931; Gardner, 1935; Stenzel, 1940; Kauffman, 1977; Sohl, 1977; Saul, 1983; Squires, 1988). Because of their widespread occurrence, fossil turritellines have been used frequently for paleoenvironmental analysis via stable isotopes (Andreasson & Schmitz, 1996, 1998, 2000; Jones & Allmon, 1999; Schmitz & Andreasson, 2001). Living turritelline species occur widely throughout much of the world's seas, and are among the most abundant gastropods in many places where they occur (reviewed in Allmon, 1988). Recent compilations (Vos & Gofas, 2009; Allmon, 2010) record approximately 1,700 fossil and living species and subspecies names, which may translate into as many as 150 valid living and perhaps 800 valid fossil species. Turritellines are also of evolutionary interest because they are one of a small number of gastropod clades that has apparently independently developed suspension feeding (DeClerck, 1995). Humans and turritellines are also interconnected in a number of ways. Turritellines are locally important for artisanal fisheries, especially in parts of Asia, and are exploited for the shell trade in many areas (both of these uses are underdocumented; Carpenter & Niem, 1998: 455–457). Several living species have been used as bioindicators for trace metal accumulation (Langston et al., 1999; Paul et al., 1999; Gibbs et al., 1998). At least one turritelline species (*Maoricolpus roseus* in Australia) is a serious invasive (human-introduced) pest (Bax et al., 2003; Gunasekera et al., 2005), and several others may be in serious decline as a result of human activities (Allmon, in review).

Our understanding of the basic biology of the Turritellinae, however, has not kept pace with recognition of its ecological, evolutionary, and geological importance. Ironically, this was probably in part because something *was* known about it. Until relatively recently, the ecology and environmental occurrence of modern turritellines was believed to be well understood and not very variable (Graham, 1938; Yonge, 1946). Closer examination, however, shows turritellines to be much more diverse. Although living turritellines are mostly suspension feeders and most abundant within a relatively narrow range of environmental conditions, the behavior, ecology, and environmental occurrence of the group are more heterogeneous than previously thought (Allmon, 1988), and the group has probably changed its environmental tolerances during its history (Allmon, 1992, 2007).

Living turritellines are not particularly easy animals to study. Adults are sensitive to exposure to air (Avens & Sleigh, 1965) and high temperatures (pers. obs.), which makes them difficult to transport from the field to aquaria. They are also extremely difficult to raise from eggs beyond the late veliger stage (Wright, 1956; Probst & Crawford, 2008). Despite these difficulties, however, a great deal of information exists about numerous aspects of their biology and paleobiology, although most of it is widely dispersed in the literature. More than two decades ago, I summarized the then-current state of knowledge of the ecology of living species of the group, based on both the scattered published sources and new observations (Allmon, 1988). Since then, considerable new information has become available on the biology of many living and fossil turritellines. Of equal or greater importance, the maturation of internet databases and search tools has made compilation of natural history information much easier than ever before. I have therefore been able to locate isolated bits of data, such as stomach contents of predators, in sources that would otherwise likely have never come to my attention. Utilizing these search tools in this way is a major, but so far underexploited, research approach for biologists.

The present paper is thus not only an update and expansion of that earlier review, it is also an attempt to stimulate other workers to produce similar reviews of the natural history of other marine gastropod groups. Only a few such surveys exist (Thompson, 1958; Paine, 1965; Ghiselin & Wilson, 1966; Peron & Turner, 1977; Harasewych, 2002; Trowbridge, 2002). As a consequence, malacologists and other biologists lack easy access to information that could be of enormous value in developing and testing ideas about the ecology, conservation, evolution, and other areas of biology of one of the most diverse groups of organisms.

SYSTEMATICS

Any survey of the natural history of turritellines takes place against a backdrop of very inadequate systematic knowledge. The family Turritellidae (Table 1) appears to be a well-defined monophyletic group within the Cerithioidea (Houbrick, 1988), but its phylogenetic relationships with other cerithioid families remain unclear (Simone, 2001; Lydeard et al., 2002; Bandel, 2006). The most recent attempt at comprehensive systematic review of the family (Marwick, 1957a) divided Turritellidae into four subfamilies (Turritellinae, Protominae, Pareorinae, and Turritellopsinae), based almost exclusively on shell characters (see also Garrard [1972] for review of Australian species). A fifth subfamily, Orectospirinae, was proposed by Habe (1955) based on radular and opercular characters. Dall (1913) assigned the sessile, vermiform *Vermicularia*, which had been placed in Vermetidae, to its own family Vermiculariidae. Morton (1953) recognized Vermiculariinae as a subfamily within Turritellidae.

The reality of these subfamilial taxa as monophyletic groups, however, remains almost completely untested. It is, however, generally accepted that certain genera are *not* turritellines (e.g., *Mesalia* Gray, 1847 [see Squires & Saul, 2007]; *Tachyrhynchus* Mörch, 1868; *Turritellopsis* Sars, 1878; *Orectospira* Dall, 1925; and *Pareora* Marwick, 1931 [see Marwick, 1957a]), based mostly on shell characters but also on some anatomical data. These genera will therefore not be discussed further here. Several other genera (e.g., *Protoma* Baird, 1870; and *Zaria* Gray, 1847) are at least conchologically ambiguous. The single molecular phylogenetic study on the group (Lieberman et al., 1993) reveals that *Vermicularia* nests within other more conventional turritelline taxa, and this is consistent with data on soft anatomy (Morton, 1953; Hughes, 1985; Bieler & Hadfield, 1990); *Vermicularia* will therefore be considered as a turritelline here.

Based on this admittedly very incomplete understanding, the following discussion will be restricted to Turritellinae as listed in Table 1, keeping in mind that most of the genera/subgenera listed there are inadequately defined (reviewed by Allmon, 1996). Indeed, the genus *Turritella* has been called a "wastebasket" (Plotnick & Wagner, 2006) or "archetypal" (Nützel, 2005) genus because it is frequently applied uncritically, essentially as a "form genus" (*sensu* Sylvester-Bradley, 1954), to any turritelline-shaped gastropod shell. In the fossil record, turritellines are so widespread and abundant that the genus name "*Turritella*" is commonly used by geologists to designate not just most turritelline-shaped fossils, but also entire rock layers (see Allmon, 2007, for further discussion). This is despite the fact that it has long been widely accepted among systematists that the genus name *Turritella* Lamarck, 1799 (type species *Turritella terebra* (Linnaeus, 1758)) should not be applied to most of these species (Palmer, 1937; Marwick, 1957a). The species *T. terebra* itself is not well-known ecologically or systematically. A recent review of this species (Allmon et al., in review) has clarified its identify, geographic distribution, and aspects of its morphology, but the implications of these results for genus-level systematics remain to be explored fully.

The family Turritellidae was long reported to have originated in the late Paleozoic (e.g., Knight et al., 1960: 316; Sepkoski, 1982: 28), and the genus *Turritella* is still occasionally cited from the pre-Cretaceous (e.g., Fursich, 1984). Bandel (2006: 94) recently stated that "Turritellidae in a shell coquina are present from mid Jurassic onwards" … in the Middle Jurassic of Madagascar, but gave no details. In a personal communication (6/11/11) he clarified that this statement needs to be confirmed by new collections. It now seems clear, however, that the oldest definite representatives of the subfamily Turritellinae as discussed herein (and perhaps the family as well) are from the Early Cretaceous (Valanginian Stage) of France and Poland (Bandel, 1993; Tracey et al., 1993; Schröder, 1995; Kaim, 2004).

ABIOTIC ENVIRONMENT

Depth

Living turritelline species generally inhabit depths of 10–100 m, but a number of species live either in very shallow water (< 10 m) or in very deep water (> 200 m) (Allmon, 1988). For example, *Turritella cingulata* G. B. Sowerby I, 1825, in Chile, *Maoricolpus roseus* (Quoy & Gaimard, 1834) in New Zealand, and *T. duplicata* (Linnaeus, 1758) in Thailand occur regularly in the intertidal zone (Allmon, 1988, pers. obs; R. Waite, pers. comm.), and *T. gonostoma* Valenciennes, 1849, in the Gulf of California has been observed frequently in water less than two meters deep (Allmon, 1988; Allmon et al., 1992). Several species, on the other hand, (e.g., *Colpospira (Acutospira) smithiana* (Donald, 1900) and *C. (A.) yarramundi* Garrard, 1972, in Australia; and *T. yucatecanum* (Dall, 1881) in the Caribbean) occur at depths exceeding 500 m; *C. (Ctenocolpus) curialis* (Hedley, 1907) in Australia) apparently normally inhabit depths as great as 1,200–1,500 m (Allmon, 1988, and references therein). Although adequate data are not available for many species, it appears that at least some are able to live across a range of depths; *M. roseus*, for example, has been reported alive from depths from intertidal to > 200 m (Gunasekera et al., 2005).

Temperature

Turritellines were formerly treated by many authors as a typically "warm-water" group (Merriam, 1941), but this was based almost completely on their higher modern species diversity in lower latitudes, particularly in the southwestern Pacific (Allmon, 1988; Hendy & Allmon, 2007). Actual temperature measurements for living species show that a few do occur regularly in temperatures above 20°C (e.g., *Turritella variegata*; Bandel & Wedler, 1987), but these appear to be exceptions rather than representative of the group as a whole; most species actually prefer relatively cool water temperatures (< 20°C) (Allmon, 1988). Several recent authors have, in fact, treated fossil turritellines as typical of "cold" waters (Majima, 1985: 116; Kanazawa, 1990; Kim et al., 1999; Kitamura et al., 2000; Abdelhady, 2008).

It is also now clear that the temperature tolerance/preference of the group has changed (from warmer to cooler) during its history. This conclusion is based on (1) the occurrence of high abundances of turritellines in carbonate sedimentary environments only in the Cretaceous and Paleogene (Allmon, 2007), and (2) oxygen isotope paleothermometry of individual fossil turritellines from these ages indicate that they thrived in considerably warmer temperatures than they do today (e.g., Middle Eocene of the U.S. Gulf Coastal Plain – 19°C winter and 27–28°C summer [Andreasson & Schmitz, 2000]; mid-Paleocene of Denmark – 23.4°C winter and 28.5°C summer and [Thompson, 2000]).

Salinity

Merriam (1941: 10) stated that turritellines are animals of normal marine salinities and cannot tolerate brackish and estuarine environments. This appears to be the case for most living and fossil species (Allmon, 1988), but at least some living species appear to thrive under less-than-full-marine salinity. Around the British Isles, for example, Shumway (1979) found that *Turritella communis* Risso, 1826, was tolerant of salinity as low as 65% seawater (ca. 24 ppt), and Avens & Sleigh (1965) found that the same species remained active at salinities as low as 50% seawater (ca. 18 ppt). In waters around Hong Kong, turritellines (listed as either *T. terebra* (Linnaeus, 1758), or *T. bacillum* Kiener, 1843) have been frequently reported as abundant (Wu & Richards, 1981; Hickman, 1983; Shin, 1983; Taylor, 1994; Leung & Morton, 2003; Shenzhen Port Tonggu Channel Developing Office, 2003). These waters are heavily influenced by freshwater input from the Pearl River, which is the second largest in China, and regularly have salinities well below 30 ppt, especially in the summer because of increased runoff associated with the southwestern monsoon (Wu & Richards, 1981; Larsen et al., 2005). Similarly, Blay & Dongdem (1996) reported abundant occurrence (44/m^2) of *T. annulata* Kiener, 1843, in a coastal lagoon in Ghana, West Africa, at salinities as low as 12–15 ppt. Several fossil turritelline occurrences have also been interpreted as representing brackish, estuarine, or variable-salinity conditions (Funder et al., 2002; Latal et al., 2006; Naughton et al., 2007).

Nutrients

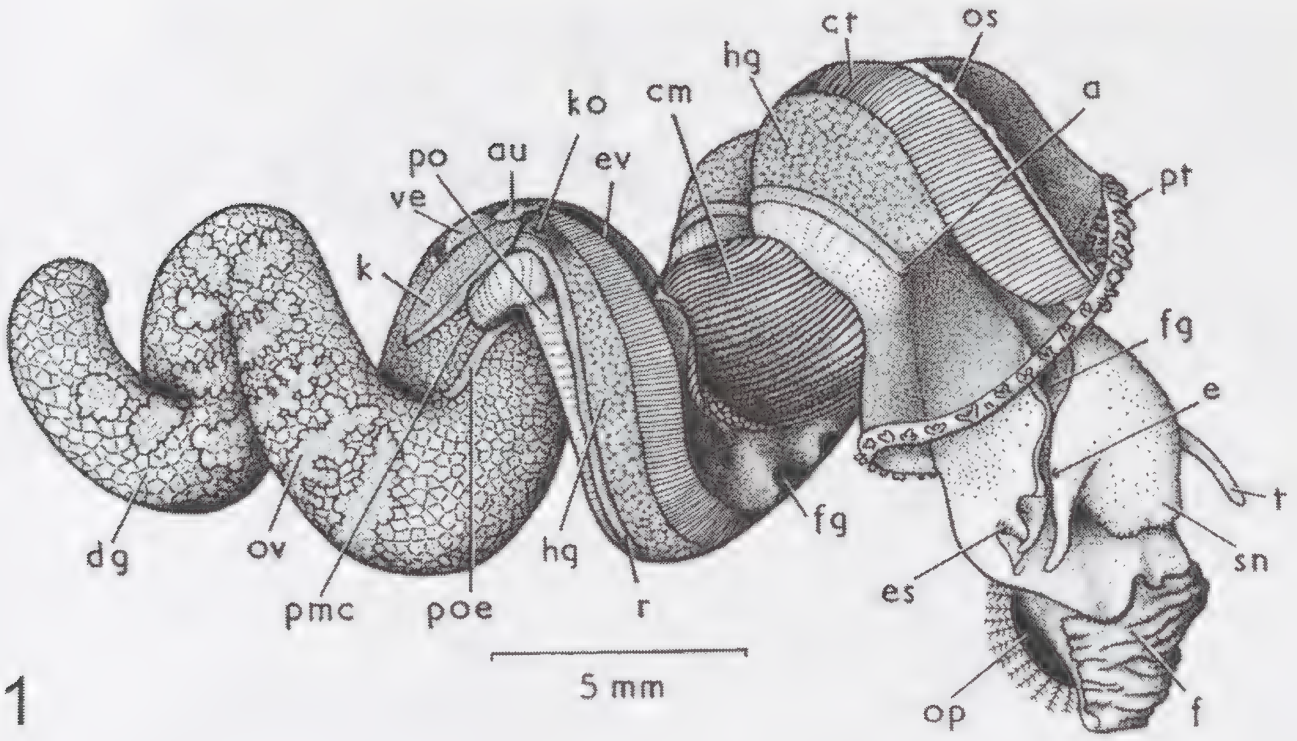
Although few direct measurements are available, a variety of proxy and circumstantial evidence supports the conclusion that high abundance in living turritellines is coincident with high levels of nutrients and primary productivity (Allmon, 1988; Allmon et al., 1992, 1994). This evidence can be grouped into at least three categories: (1) turritelline-dominated assemblages frequently occur in or near areas of moderate to high upwelling or terrestrial runoff (e.g., New Zealand, northern Gulf of California, Chile, west Africa, northern Venezuela, Hong Kong); (2) turritellines are rare or absent in modern oligotrophic, warm-water marine environments; and (3) turritellines are mainly suspension feeders and so would likely benefit directly from higher levels of planktonic productivity. For example, turritellines are relatively abundant in areas of the modern Adriatic in which nutrients are relatively high, and rare or absent where they are low (McKinney, 2003). Living turritellines are extremely rare on Pacific atolls, but are relatively abundant on Tarawa (Paulay, 1997, 2000), which is located in in the nutrient-rich waters of the equatorial upwelling zone, providing for much higher levels of productivity than typical of Oceania (Kimmerer & Walsh, 1981; Kimmerer, 1995; Paulay, 1997; Paulay & Kerr, 2001).

ANATOMY

Soft Parts

Soft-part anatomy is known in detail for only one turritelline species: *Turritella communis* from the northeastern Atlantic (Randles, 1900, 1902; Graham, 1938; Yonge, 1946; Johansson, 1946; Fretter & Graham, 1962, 1981; Kennedy, 1995). Less comprehensive information is available for a few other species: *Gazameda gunnii* (Reeve, 1849) from Australia (Carrick, 1980a, b); *Maoricolpus roseus* from New Zealand and Australia (Allmon et al., 1994; Bax et al., 2003); *T. gonostoma* from the Gulf of California (Allmon, 1988; Allmon et al., 1992); *T. terebra* from Hong Kong (Hickman, 1983); *T. banksi* Reeve, 1849, from Panama (Allmon, unpublished observations); *Vermicularia spirata* Philippi, 1836 (Morton, 1953; Bieler & Hadfield, 1990); and *V. pellucida* Broderip & Sowerby, 1829 (Hughes, 1985; Healy & Wells, 1998) (Figs. 1–11.) The description below is based on these sources.

The head-foot has a short, wide snout, and a pair of long cephalic tentacles, each with an eye situated near the base. The foot itself is relatively small, with a ciliated groove on the right side. The operculum is round, multispiral, and flexible, and usually bears peripheral bristles, except in *Vermicularia* (Morton, 1953).



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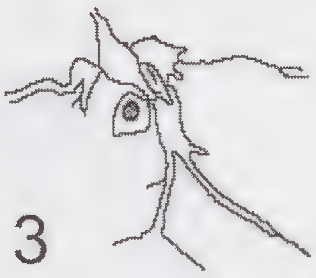

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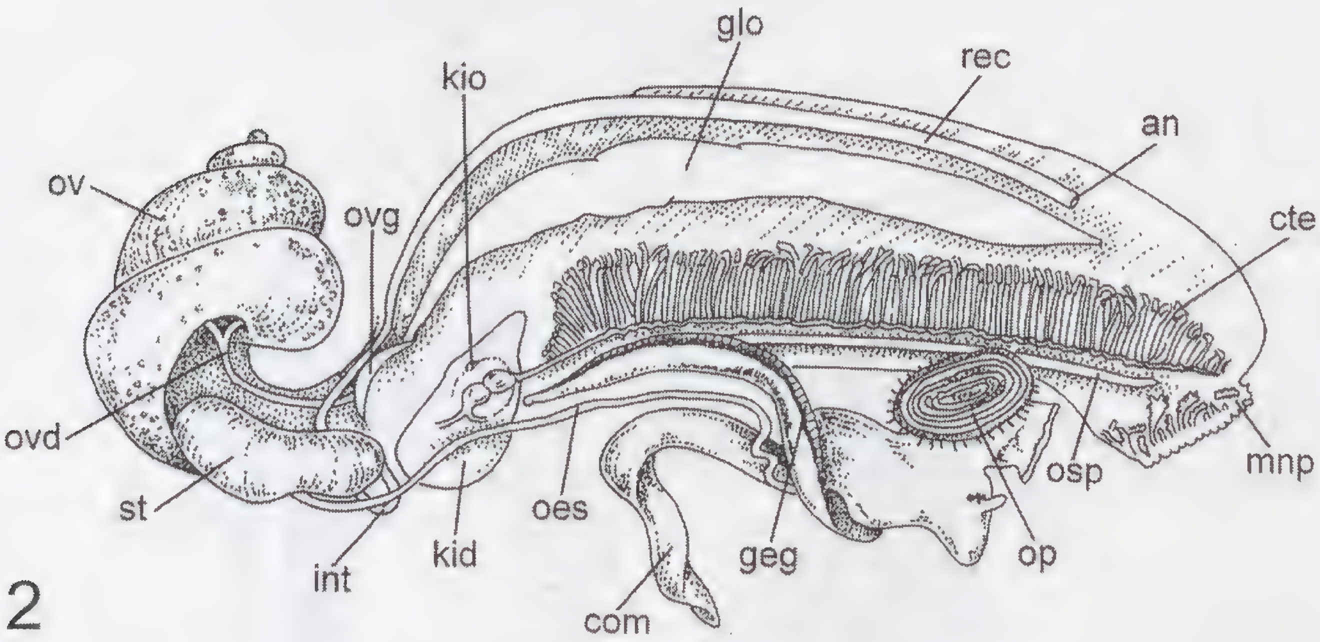

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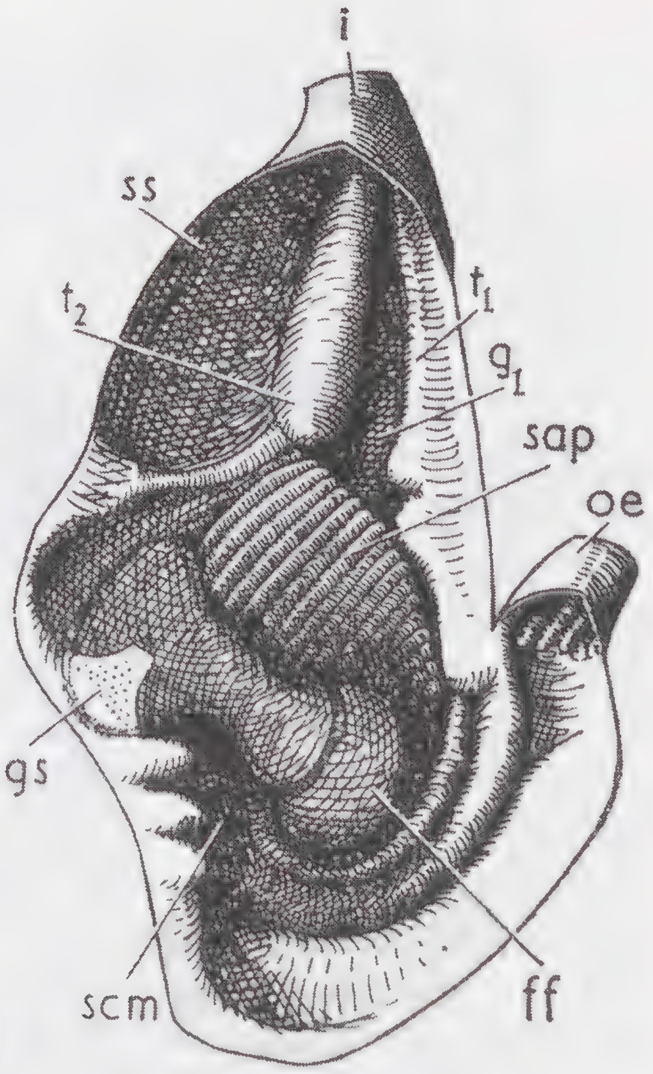

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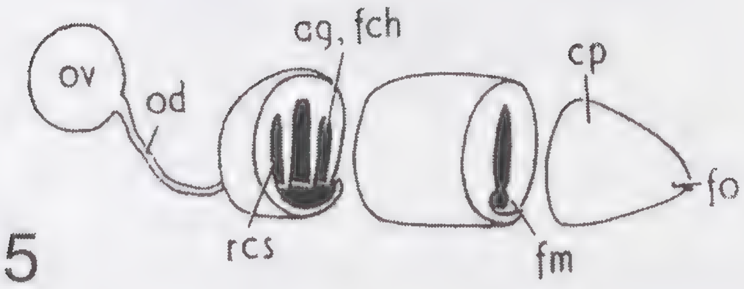

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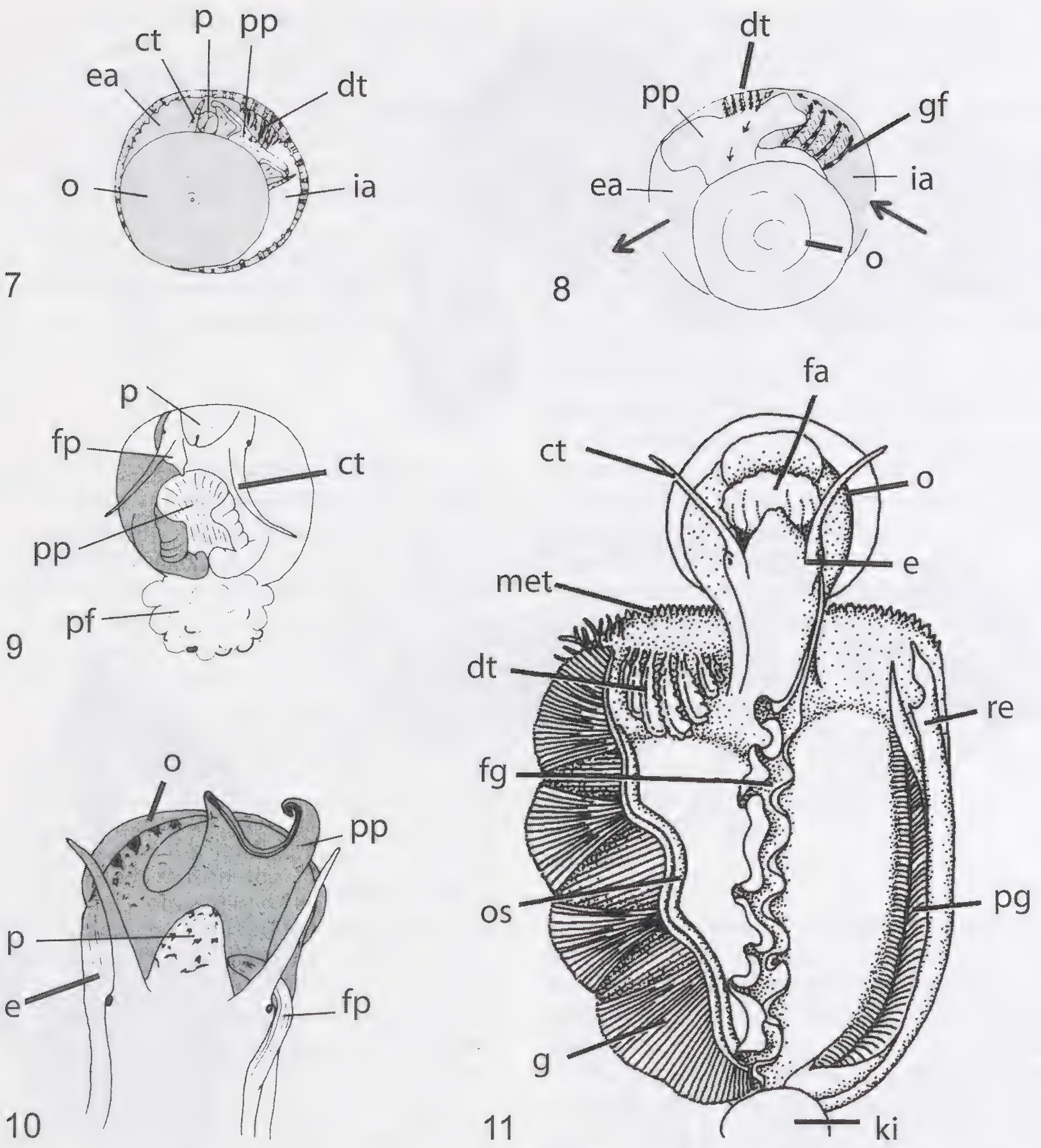
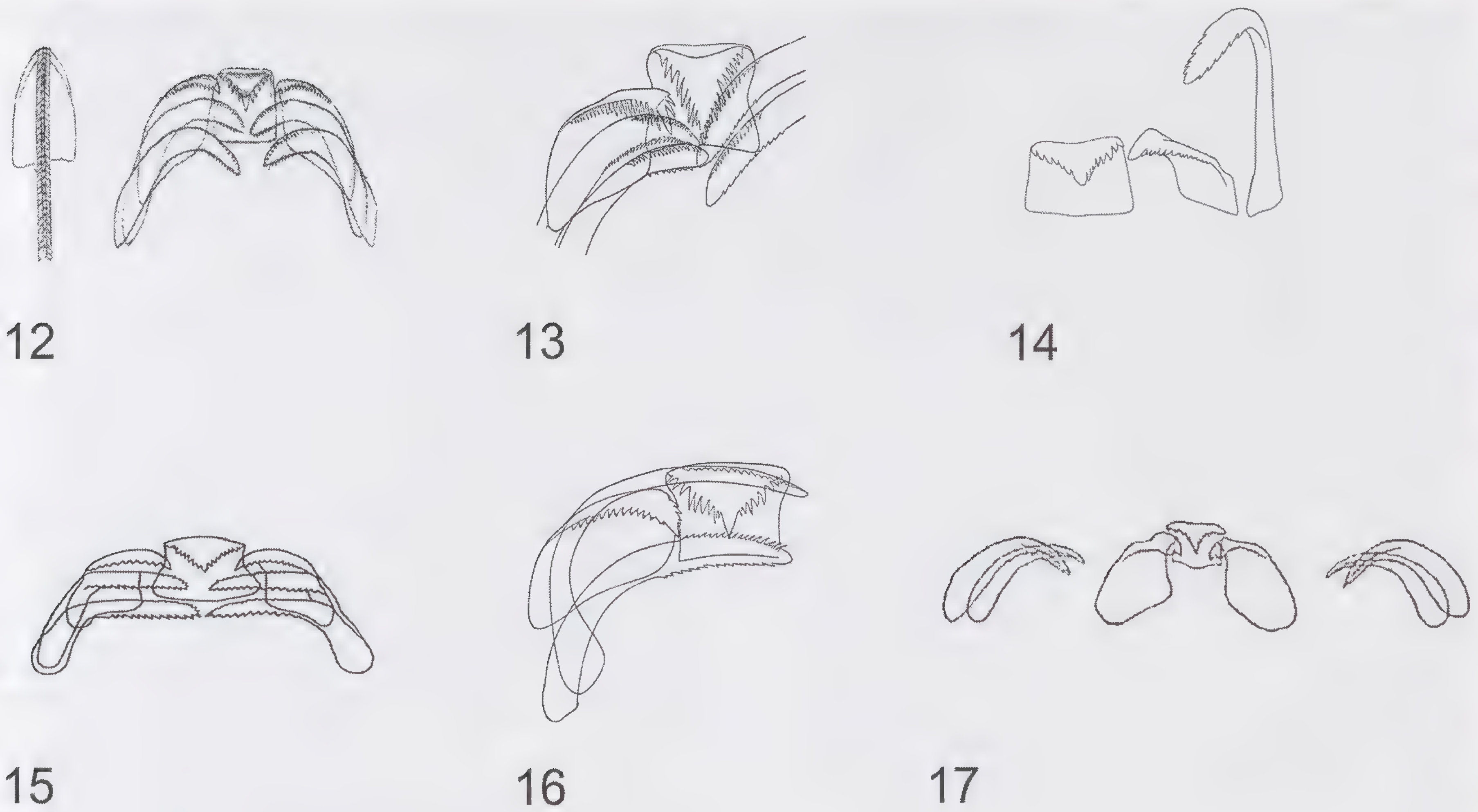
FIGS. 1–6. Soft-part anatomy of *Turritella communis*. FIG. 1: Entire animal, extracted from its shell (a = anus, au = auricle, cm = columellar muscle, ct = ctenidium, dg = digestive gland, e = eye, es = exhalent siphon, f = foot, fg = food groove, hg = hypobranchial gland, k = kidney, op = operculum, os = osphradium, ov = ovary, pmc = posterior limit of mantle cavity, po = pallial oviduct, poe = posterior esophagus, pt = pallial tentacles, r = rectum, sn = snout, t = tentacle, ve = ventricle) (modified from Fretter & Graham, 1962, fig. 57); FIG. 2: Anatomy of a female of *T. communis* with the mantle cavity opened, at approximately the same scale as FIG. 1 (an = anus, com = columellar muscle, cte = ctenidium, geg = genital groove, glo = glandular portion of oviduct, int = intestine, kid = kidney, kio = kidney opening, mnp = mantle papillae, oes = esophagus, op = operculum, osp = osphradium, ov = ovary, ovd = oviduct, ovg = oviducal gland, rec = rectum, st = stomach) (from Healy & Wells, 1998, after Randles, 1900); FIG. 3: Sketch of a portion of the nervous system, including an otocyst (*ot*) (modified from Randles, 1900); FIG. 4: Sketch of the nervous system, seen from above (modified from Randles, 1900); FIG. 5: Female genital duct. (ag = albumin gland, cp = capsule gland, fch = fertilization chamber, fo = genital duct opening, od = oviduct, ov = ovary) (from Fretter & Graham, 1962: fig. 186); FIG. 6: Stomach (dd = opening of duct of digestive gland, ff = fold emerging from spiral caecum, g1 = intestinal groove, gs = gastric shield, i = intestine, oa = esophageal aperture, sap = sorting area, scm = spiral caecum, ss = style sac region, t1 = major typhlosole, t2 = minor typhlosole) (from Fretter & Graham, 1962: fig. 121C).



FIGS. 7–11. Soft-part anatomy of *Vermicularia spirata*. FIG. 7: View looking into the aperture, showing operculum and pappilated margin of the mantle cavity; FIG. 8: Same view, showing movement of particles and mucus over the ctenidial filaments and onto the sole of the foot, where they accumulate as pseudofeces. Arrows indicate direction of water movement; FIG. 9: Pseudofeces collecting between the sole of the foot and the opercular rim; FIG. 10: Dorsal view of head, showing proboscis, propodium, food groove papilla, and operculum; FIG. 11: Female of *V. spirata*, with the mantle cavity opened, showing the pallial gonoduct. Abbreviations: ct = cephalic tentacle, dt = dorsal pallial tentacle, e = eye, ea = excurrent aperture, f = foot, fg = food groove, fo = foot, fp = food groove papilla, g = ctenidium; gf = ctenidial filament, ia = incurrent aperture, ki = kidney, met = mantle-edge tentacle, o = operculum, os = osphradium, p = proboscis, pp = propodium, pf = pseudofeces, pg = pallial gonoduct, re = rectum. FIGS. 7–10 modified from Hughes, 1985; FIG. 11 modified from Bieler & Hadfield, 1990.

The mantle cavity is elongated, and divided into two compartments by the attachment of the mantle to the cephalopedal mass in the middle of the animal's dorsum. The entrance to the mantle cavity, on the animal's left, is surrounded by rows of papillae or tentacles, which prevent the entrance of large particles. Inside the larger left compartment of the mantle cavity, smaller particles in the incurrent stream are caught on the single elongate ctenidium. The

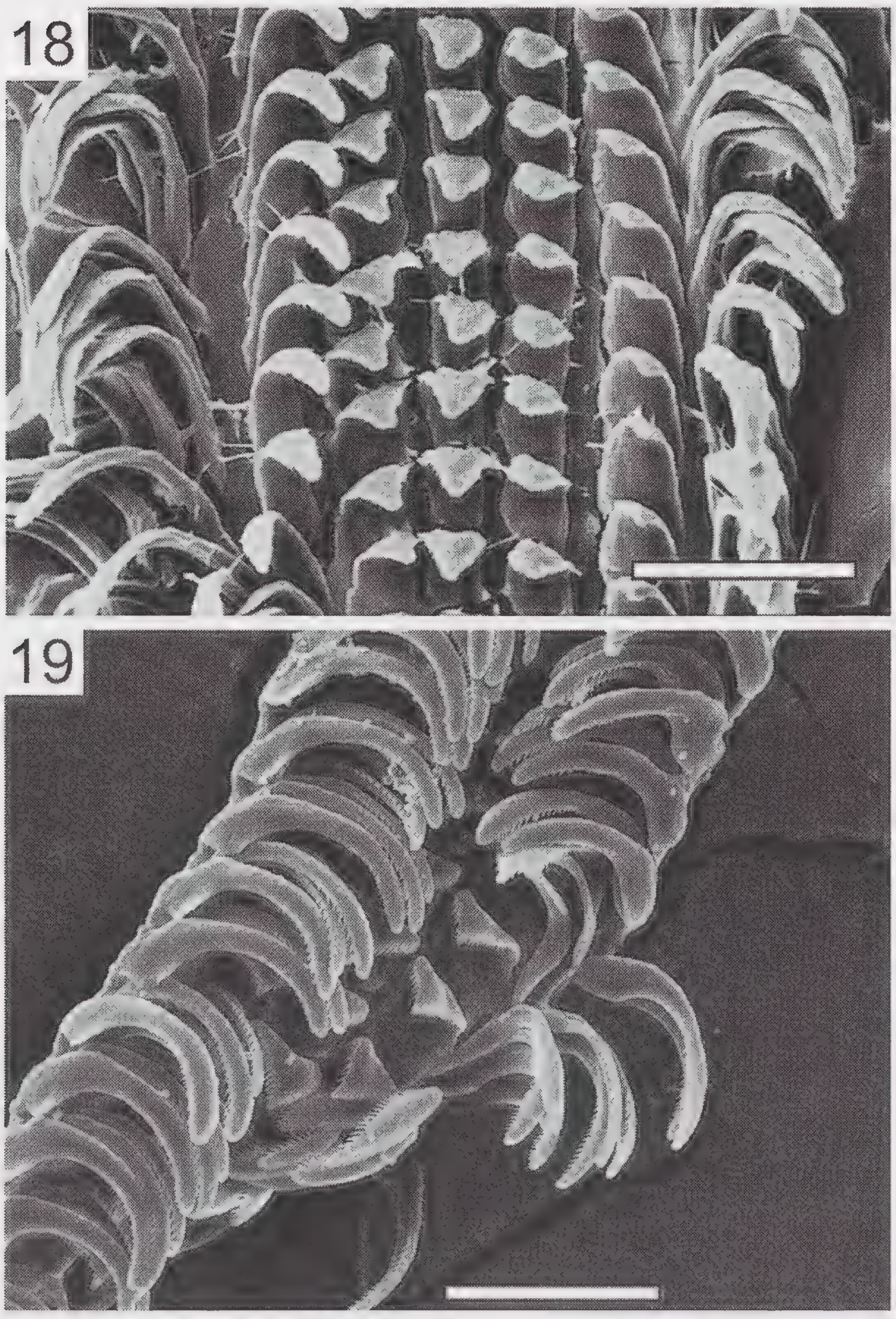


FIGS. 12–17. Previous drawings of turritelline radulae. FIG. 12: *T. communis* from Sars (1878); FIG. 13: *T. communis* from Morton (1953); FIG. 14: *T. communis* from Bandel (1984); FIG. 15: *T. spectrum* Reeve, 1849 (=? *T. terebra*) redrawn from a drawing associated with specimen in the collection of the Academy of Natural Sciences, ANSP 38621; FIG. 16: *Vermicularia spirata* from Morton, 1953; FIG. 17: *Colpospira (Ctenocolpus) australis* (Lamarck, 1822) modified from Randles, 1900.

ctenidial filaments are narrow, elongated, and laterally flattened. Each filament is attached to the ctenidial axis by its base and fixed to the adjacent mantle skirt on the right of the axis by the basal third of its dorsal surface. In this way, the long axes of the filaments lie roughly parallel with the roof of the mantle cavity and their tips curve over to rest on the floor. Captured food particles are passed by ciliary action to the tips of the gill filaments, which then convey them into a deep groove in the mantle floor. There the particles are trapped in a mucous strand or rope secreted by a combination of the hypobranchial gland, a strip of cells ("confusingly termed" [Hughes, 1985: 323] the "endostyle") along the ctenidial axis, and by the gill filaments and the walls of the groove. In this food groove, the mucous strand is constantly rotated and eventually reaches a peripheral spoon-shaped fold into which the animal extends its radula to gather the accumulated food. Inside the mouth is a pair of thin, weak jaws.

Surprisingly little has been published about turritelline radulae since the brief descriptions of Cooke (1895) and Randles (1900). Cooke noted that the turritelline radula is small and taenioglossate; that is, characterized by seven teeth per row, including a "central tooth of very variable form, the prevailing type being multicuspid, the central cusp the largest, on a rather broad base; a single lateral, which is often a broad plate, more or less cusped, and two uncini [marginal teeth], rather narrow, with single hooks, or slightly cusped" (1895: 223). Cooke also remarked on the turritelline radula's relatively small size, an observation repeated by Graham (1938: 458–459) for *Turritella communis*. Graham noted that a "generally simple and reduced radula bearing fine teeth" would be consistent with the species' presumed exclusively suspension-feeding habit, and is "most frequently used for raking in the mixture of food and lubricating material brought to the mouth ready mixed along the ciliated groove and not for the independent collection of food". Carrick (1980a, b) similarly noted that the radula in *G. gunnii* is reduced relative to other cerithioids, but also that it does show patterns of wear that apparently reflect rasping against the larger sediment particles entrained by the mucus rope.

Randles noted that "there is a considerable amount of variation in the radulae of different species" of turritellines (1900: 58; Figs. 12–17). All species for which data are available have a single median or rachidian tooth, and a single lateral tooth and two marginal teeth to each side (i.e., 2 + 1 + 1 + 1 + 2 formula) (Figs. 12–19). Boss (1982) and Healy & Wells (1998), however, stated (without providing specific sources) that the number of marginals varies from zero to three within the family (this information may have originated with Troschel [1856] [R. Bieler, pers. comm., March 2011]). The rachidian tooth is quadrangular in shape, with a relatively broad, straight base and a reflexed triangular apex, the margin of which bears a large central cusp bordered laterally by numerous smaller denticles. The lateral teeth have finely denticulate free margins, and vary in size from approximately equal to considerably larger than the rachidian. The marginals are sickle- or scythe-shaped, their edges "being serrated in such a manner as to impart a feathery appearance to the tooth when that is turned over and seen in surface view" (Randles, 1900: 58).



FIGS. 18–19. Scanning electron micrographs of turritelline radulae. FIG. 18: *Turritella nzimaorum* Ryall and Vos, 2010, from Ghana. Scale bar = 50 µm (from Ryall and Vos, 2010); FIG. 19: Previously unpublished image of the radula of *Turritella trisulcata* Lamarck, 1822, from the Red Sea. Scale bar = 50 µm (specimen in the collection of the Paleontological Research Institution).

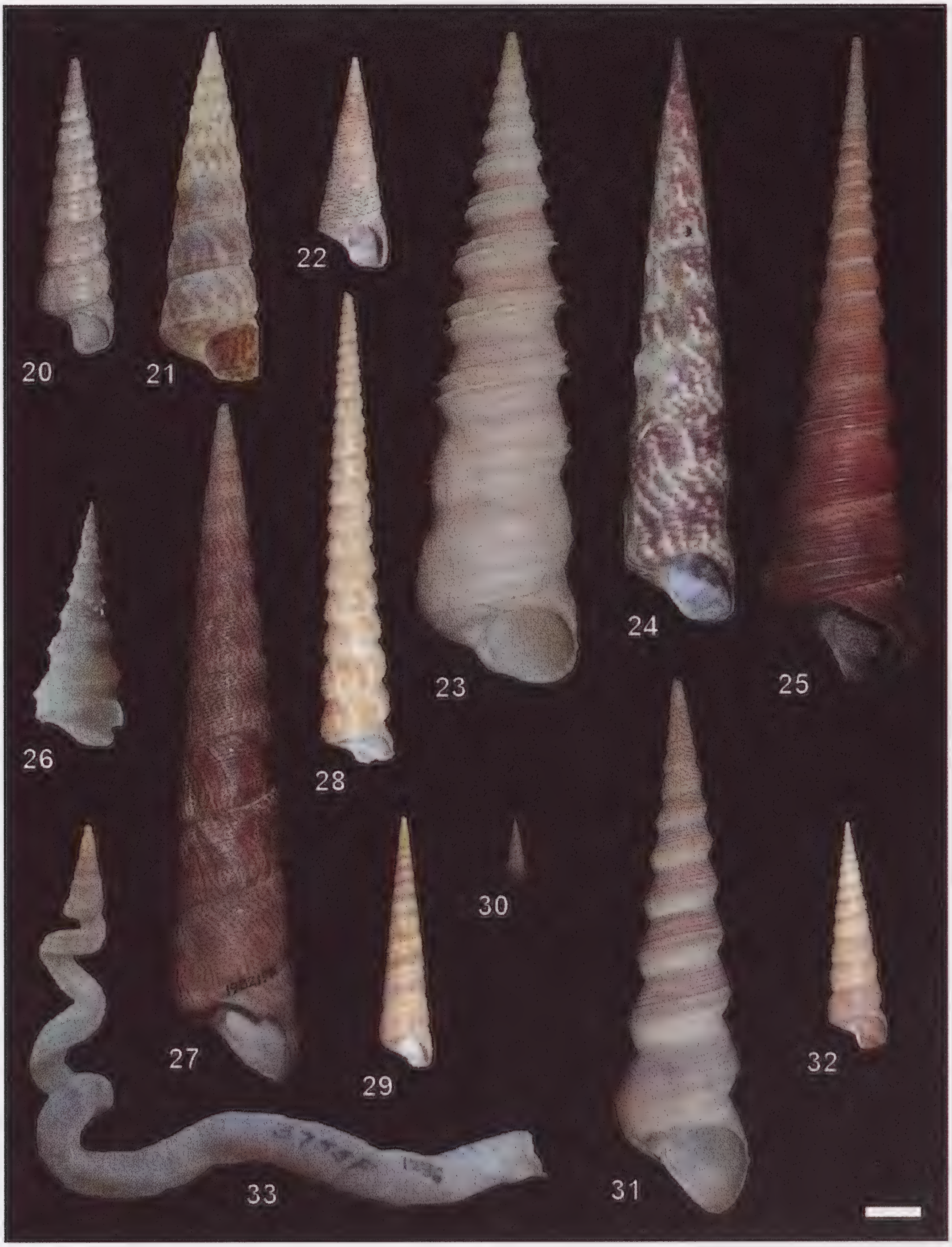
Scanning electron micrographs of turritelline radulae have only recently become available (Figs. 18, 19). These images confirm most earlier observations. The radular ribbons are indeed very small, measuring approximately 150 µm wide. The rachidian and lateral teeth are of approximately equal size and are finely denticulate, and the marginals are narrow and elongate, and finely-denticulate.

The esophagus is a straight tube with a dorsal food channel (A. Graham, 1939). It leads to a relatively complex stomach (Seshaiya, 1932; Fretter & Graham, 1962; Fig. 6). A gastric shield covers much of the stomach wall, and a crystalline style abuts the shield. (The crystalline style – a stiff rod of mucoprotein which, as it rotates and dissolves in the stomach, dissolves and releases digestive enzymes – is present in almost all bivalves and most suspension feeding gastropods [Yonge & Thompson, 1976; Purchon, 1977; Hughes, 1986; DeClerck, 1995].) An area of folds on the stomach wall acts as a sorting area for the food particles.

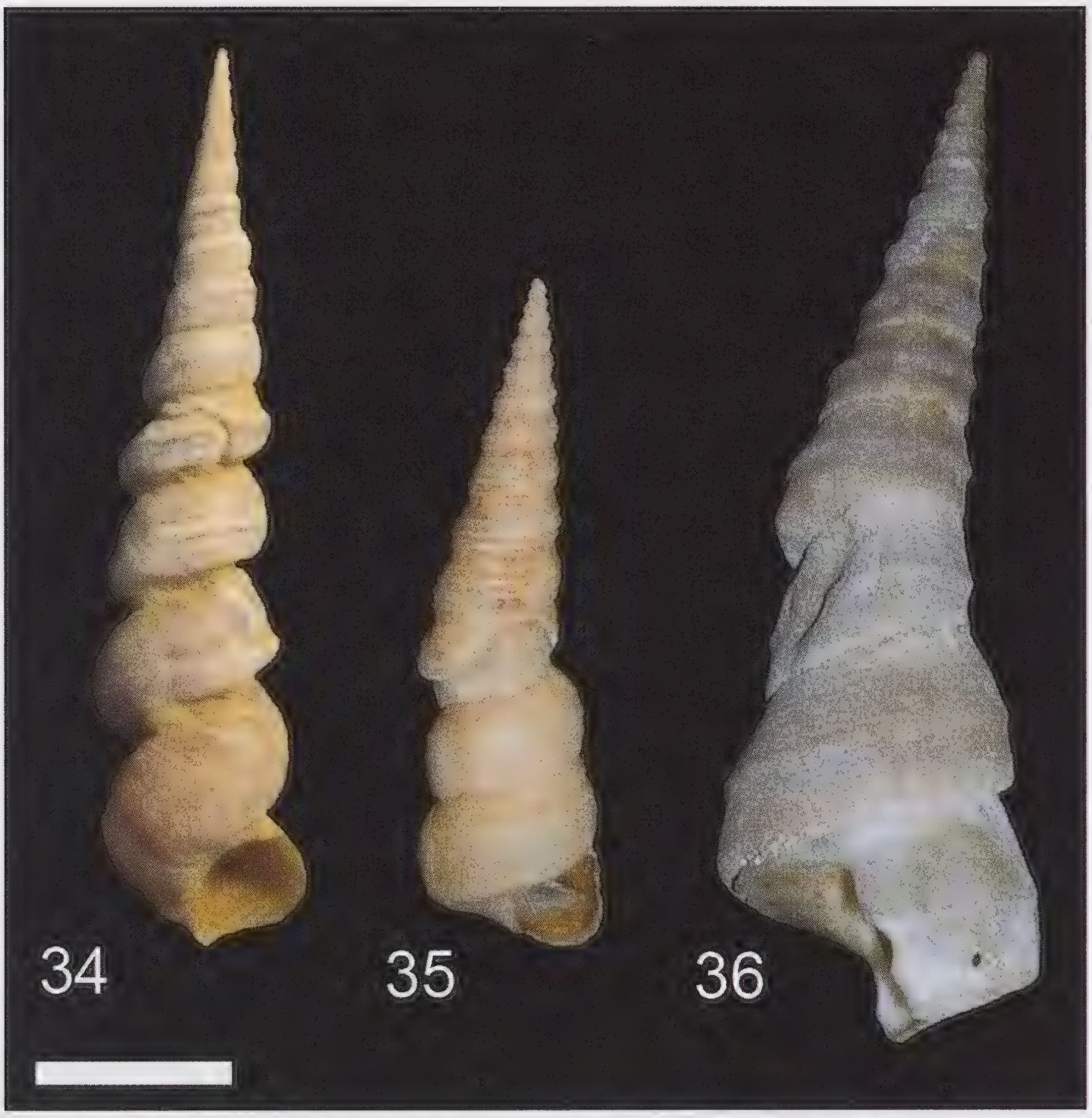
The high spire of the turritelline shell is filled almost to the apex with a tightly-packed visceral mass, consisting of two closely-appressed organs, an elongated digestive gland and an elongated gonad (Figs. 1, 2).

Water currents exit the mantle cavity on the right side of the animal via an excurrent siphon formed by folds of the mantle edge. The stream exiting this siphon is strengthened by the action of cilia over the rectum and the open pallial genital duct, so that the ovoid fecal pellets of compacted particles are expelled clear of the animal's head. Their expulsion is usually reinforced by a slight but sudden retraction of the head-foot into the mantle cavity.

Both male and female reproductive tracts have coelomic and pallial (mantle cavity) sections. There is no copulatory organ. In males, sperm is delivered from the gonad in a seminal duct, a part of which is altered into an open prostate gland. From here the sperm duct narrows and runs into the floor of the mantle cavity along a folded, ciliated groove between the right fold of the food groove and the excurrent "pseudo-siphonal process". In females (Figs. 2, 6), the coelomic oviduct leads into the hind part of the mantle cavity, which contains a developed pallial oviduct divided into medial and lateral laminae. Two pouches, a receptaculum seminis and a bursa fertilization/albumen chamber, lie on either side of the



FIGS. 20–33. Adult shells of some living turritelline species, selected to represent the group's present range of morphological variation. Scale bar = 1 cm. FIG. 20: *Turritella bicingulata* Lamarck, 1822, Azores, Natural History Museum, London (NHM) Collection; FIG. 21: *T. variegata* (Linnaeus, 1758), Venezuela, Paleontological Research Institution (PRI) Collection; FIG. 22: *Maoricolpus roseus* (Quoy & Gaimard, 1834), New Zealand, NHM Collection; FIG. 23: *T. duplicata* (Linnaeus, 1758), India, NHM Collection; FIG. 24: *T. gonostoma* Valenciennes, 1832, Peru, NHM Collection; FIG. 25: *T. terebra* (Linnaeus, 1758), Philippines, NHM Collection; FIG. 26: *T. carinifera* Lamarck, 1822, South Africa, PRI Collection; FIG. 27: *T. broderipiana* d'Orbigny, 1840, Peru, NMH Collection; FIG. 28: *T. columnaris* Kiener, 1834, Somalia, NHM Collection; FIG. 29: *Gazameda gunnii* (Reeve, 1849), Australia, NHM Collection; FIG. 30: *Stiracolpus delli* Marwick, 1957, New Zealand, NHM Collection; FIG. 31: *T. accutangula* Linnaeus, 1758, Malaysia, NHM Collection; FIG. 32: *T. communis* Risso, 1826, English Channel, NHM Collection; FIG. 33: *Vermicularia fargoi* Olsson, 1951, Florida, PRI Collection. (Photos from NHM Collection courtesy of Ursula Smith).



FIGS. 34–36. Modern turritelline shells showing aberrant morphologies following shell breakage. FIG. 34: *Turritella communis*, Adriatic Sea, PRI Collection; FIG. 35: *T. communis*, Isles of Scilly, Cornwall, England, NHM Collection; FIG. 36: *T. carinifera*, South Africa, NHM Collection. Scale bar = 1 cm.

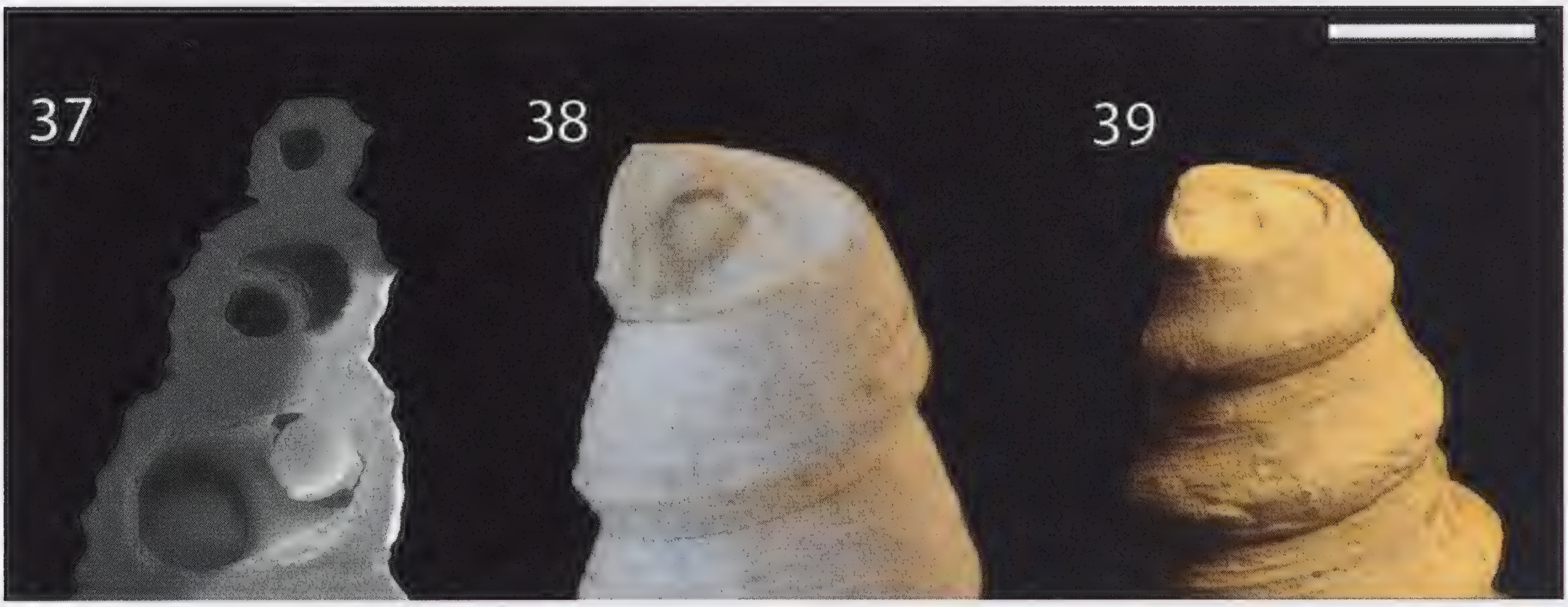
posterior pallial oviduct. A large pallial capsule gland completes the encapsulation of fertilized eggs and albumen during spawning. As is also the case for other related aphallate families (e.g., Cerithiidae, Melaniidae, Potamididae, Vermetidae), the pallial oviduct is open.

The nervous system is zygoneurous (Bouvier, 1887; Randles, 1900; Fig. 4), and has relatively long connectives between the cerebral ganglia, a subesophogeal ganglion close to the pleural ganglion, and short cerebropedal connectives (Randles, 1900). *Turritella communis* is reported to have "a single large circular otolith" (Fig. 3) (Randles, 1900: 63).

Shell

The turritelline shell (Figs. 20–33), as noted by Gould (1969: 433), has long been cited for the elegant mathematical regularity of its coiling (Moseley, 1838; Thompson, 1942). It consists of 15 to 30+ round to angulate whorls (see, e.g., whorl profile diagrams in Allmon, 1996), which succeed each other with high translation rate around the coiling axis, resulting in the characteristic high-spired "turritelliform" shape. The columella is usually indistinct. The aperture is not entire, and its inner surface bears only a slight callus. There is no discrete anterior siphonal notch.

Shell growth is indeterminate, but there are frequently signs of gerontism in the latest whorls of some species, especially slight to significant uncoiling (Pérez, 1929; Andrews, 1974). This is taken to the extreme in *Vermicularia*, which in most respects looks like a "normal" turritelline as a juvenile, but then begins to uncoil after 10–15 whorls (Gould, 1969; Hughes, 1985) and becomes completely, and usually permanently, sessile (Fig. 33). (Gould [1968] described a remarkable local population of *Vermicularia* in Bermuda, the majority of which do not uncoil



FIGS. 37–39. Apical infillings in Recent and fossil turritellines. FIG. 37: *Maoricolpus roseus*, Recent, New Zealand. Scanning electron micrograph of a longitudinal slice through the shell apex, showing three meniscate septae. Image courtesy of Ursula Smith; FIG. 38: *Turritella robusta*, Late Miocene, Panama, showing broken apex revealing meniscate septum; FIG. 39: *Kapalmerella mortoni*, Paleocene, Alabama, showing broken apex revealing amorphous infilling. Scale bars = 5 mm. All specimens in the PRI Collection.

at all as adults, but stay mostly buried in soft substratum as do other turritellines.) Uncoiling and other "abnormalities" of the turritelline shell are frequently associated with trauma (such as breakage associated with unsuccessful predation; see below) (Figs. 34–36).

Many living and fossil turritelline species show secondary internal structures in apical whorls, ranging from one or more meniscate septa to solid infillings or plugs, which seal the apex if it is broken off (decollation) (Tate, 1893; Boekschoten, 1967; Andrews, 1974; Figs. 37–39). Similar features are known in many other fossil and recent gastropod groups (Draper, 1985; Gubanov et al., 1995; Rohr & Measures, 2001). Despite their widespread occurrence, however, neither their function nor mode of formation is well understood.

At least one fossil species assigned to Turritellidae (although not necessarily to Turritellinae) shows the "agglutinating" habit – attaching shells and other objects to the outside of the shell – similar to the gastropod *Xenophora*. Shells of *Springvaleia leroyi* (Guppy, 1867) from the Late Miocene of Panama, Trinidad, and Venezuela show imprints of bivalve shells and other foreign objects on the external surface of the shell (Rutsch, 1942: 133; Weisbord, 1962: 150).

Despite their reputation for homogeneity, turritelline shells show considerable variation in shape and external sculpture (Figs. 20–33). Yet little is known about the functional morphology of these or other aspects of the turritelline

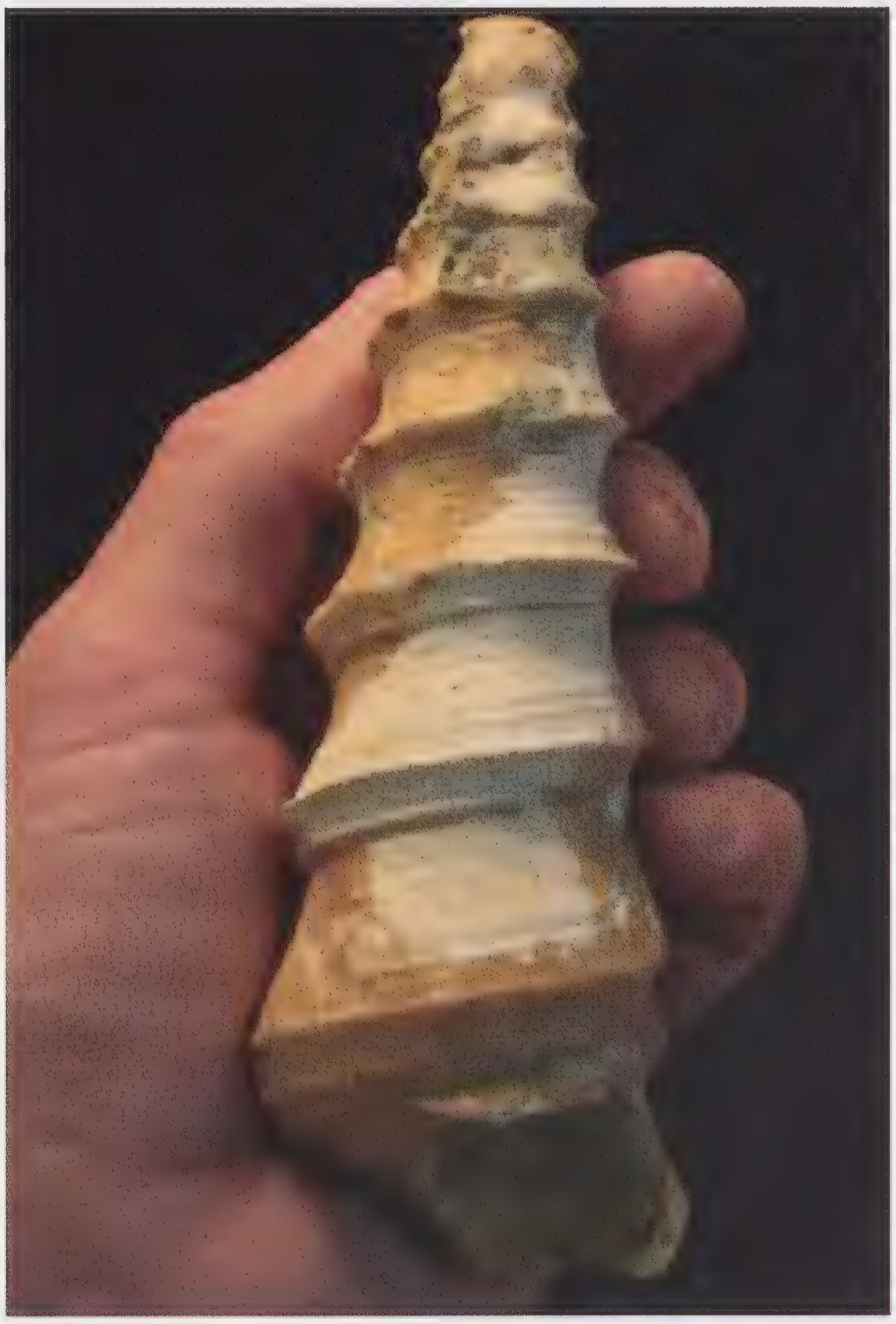


FIG. 40. A very large specimen of the largest known turritelline species: an unnumbered specimen of *Turritella robusta* in the collection of the Natural History Museum, Basel Switzerland, from the Late Miocene of the Darién region of Panama, locality 18529. Specimen is approximately 17 cm long.

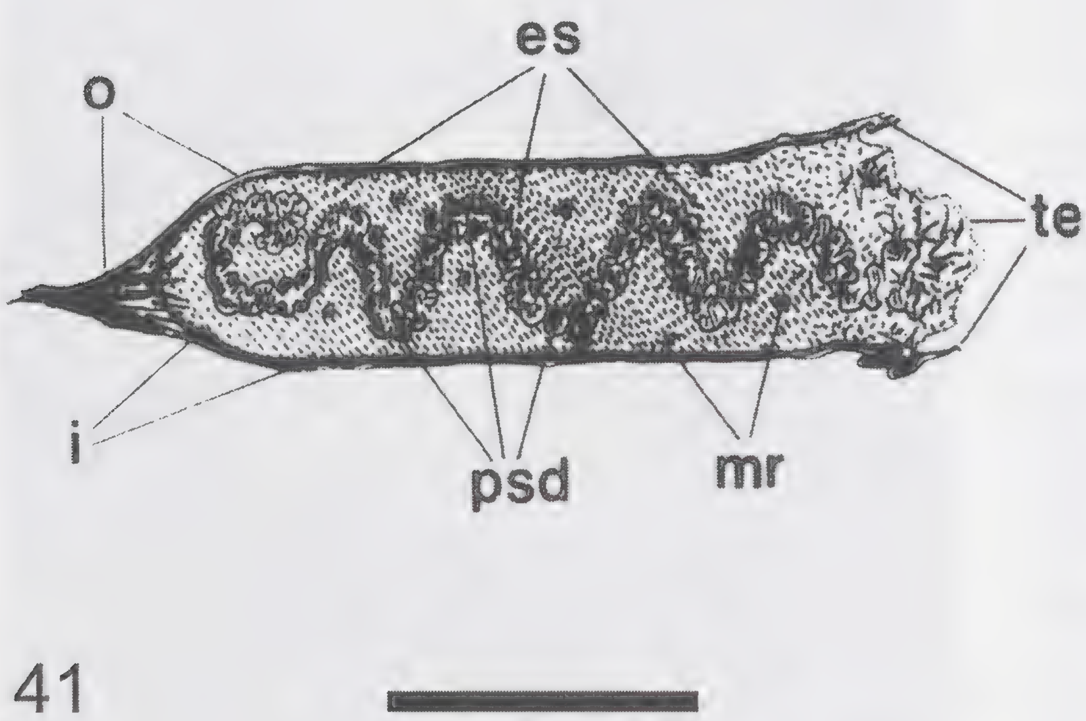
shell. Although some authors have argued that the turritelliform shell form itself may function to resist predation (by permitting deep withdrawal by the animal from the aperture) (Signor, 1985; Vermeij, 1987: 195, 220), there is no direct evidence of an anti-predatory function for any details of shell structure. Circumstantial evidence from fossils suggests that external sculpture does not have a significant anti-predatory function (Allmon et al., 1990), but this has not been tested experimentally in living species. The turritelliform shape is by definition largely isometric, but significant allometry is probably present in most species, suggesting that heterochrony may be an important evolutionary pattern in the group (Andrews, 1974; Allmon, 1994). The range of morphological variation of the shell has been examined in only two living species: *Turritella communis* (Wright, 1956; Charles, 1977), and *T. terebra* (Allmon, 1996).

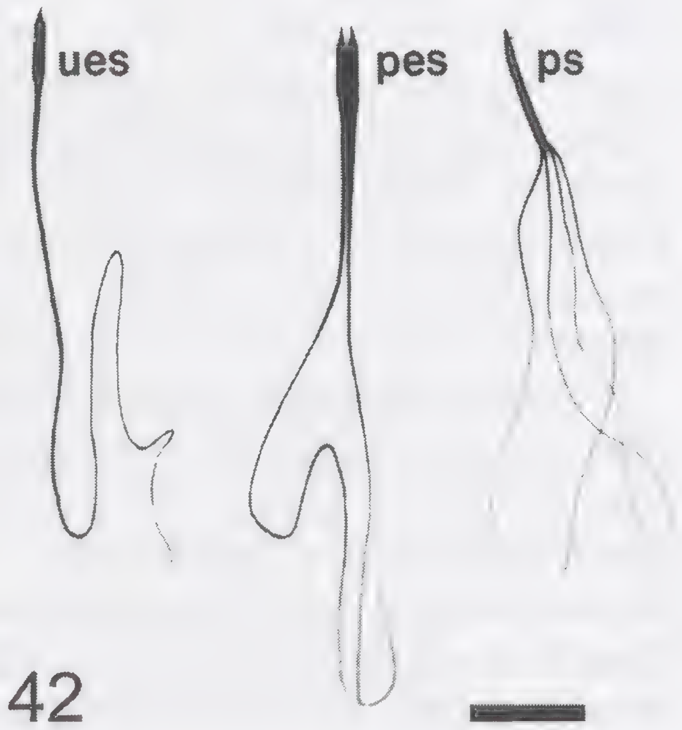
Living species range from approximately 10 to 175 mm in complete adult shell length (e.g., Figs. 20–33), with most ranging from 30–100 mm. The smallest known turritellines are probably several species of Recent *Platycolpus* from Australia (Garrard, 1972). The largest known turritelline is the fossil species *Turritella robusta* Grzybowski, 1899, from the Miocene and Pliocene of Venezuela, Trinidad, and Panama, which reached lengths of more than 200 mm (Woodring, 1957: 107; Fig. 40).

REPRODUCTION AND EARLY ONTOGENY

General Reproductive Biology

In all but two of the living turritelline species for which information is available, sexes are separate; in all known species, males are aphallate, and fertilization is internal (Allmon, 1988; Bieler & Hadfield, 1990; Kennedy, 1995; Healy & Wells, 1998). The exceptions are the Australian turritelline *Gazameda gunnii,* and the uncoiled *Vermicularia spirata*, both of which are protandrous hermaphrodites in which all hatchlings are male. In *Gazameda*, these pass through an intermediate phase during which they have both male and female anatomical features, after which individuals become and remain fully female (Carrick, 1980a, b). In *Vermicularia*, the juvenile males are free-living, and become attached to the substratum and start to uncoil about the time they undergo sex change (Bieler & Hadfield, 1990). In the two species that have been studied in most detail – *Turritella communis* from the northeastern Atlantic and *Maoricolpus roseus* from New Zealand and Australia – as well as in *V. spirata*, females are larger than males (Pelseneer, 1926; Wright, 1956; Bieler & Hadfield, 1990; Kennedy, 1995). A similar pattern of sexual dimorphism has been hypothesized for several other living and some fossil turritellines (Kotaka, 1980). In *G. gunnii*, shells of females brooding





FIGS. 41–42. *Turritella communis.* FIG. 41: Spermatophore (es = euspermatozoal mass; i = inner gelatinous wall; o = outer membranous spermatophore covering; psd = diverticular membrane containing paraspermatozoa; te = torn end of spermatophore). Scale bar = 1 mm (after Kennedy, 1995); FIG. 42: Unpaired euspermatozoon (ues), paired euspermatozoa (pes), and multiflagellate paraspermatozoon (ps). Scale bar = 10 µm (after Kennedy, 1995).

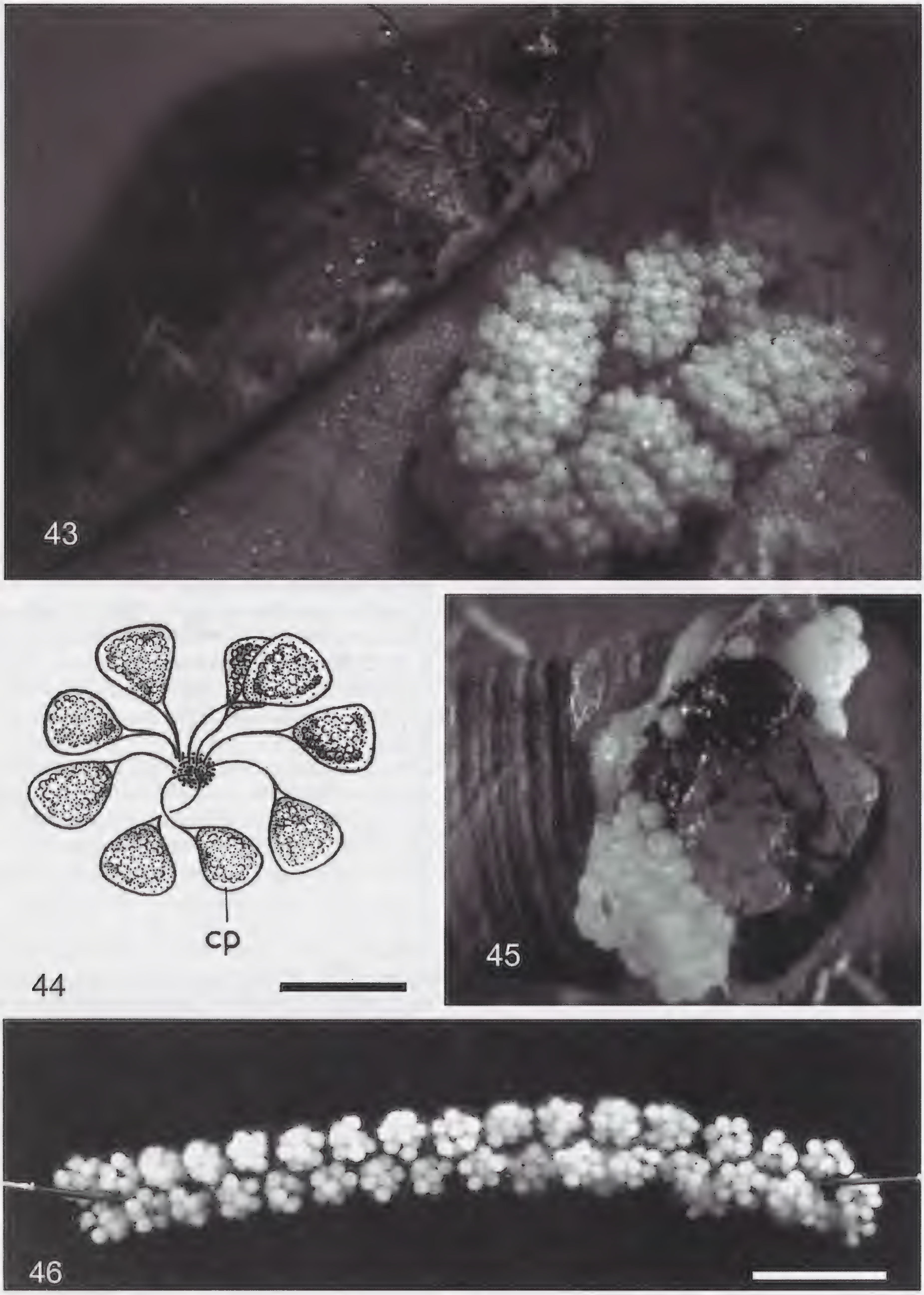
eggs or juveniles are larger and have more swollen later whorls than do males (Iredale, 1924; Merriam, 1941).

Although it has never been specifically reported, in most species sperm are assumed to be broadcast by the male into the water, and taken in by the female via her incurrent siphon (Fretter, 1953; Fretter & Graham, 1962: 361; Morton & Miller, 1968: 582). In *Turritella communis*, however, pseudocopulation (the close positioning, without intromission, of male and female to facilitate contact between eggs and sperm at the time of discharge [Thorson, 1950]), in which one or more males delivers one or more spermatophores directly to a single female, has been described in detail (Kennedy, 1995). Kennedy described "pseudocopulation groupings of 3–11 males in star-shaped arrangements" surrounding a female buried in the substratum. Males are presumably attracted by some kind of chemical signal emitted by the female, and "erupt from the sediment" and craw along the surface as far as 0.5 m to locate her. Males produce a "complex double-walled cylindrical spermatophore [3–4 mm in length; Fig. 41] containing paired and unpaired euspermatozoa, and multiflagellate paraspermatozoa" (Fig. 42). Kennedy reported that the spermatophore "is delivered to the hind part of the mantle cavity from the coelomic vas deferens and is moulded in a tight, spirally bound tubular form as it emanates on the right side of the head. A tract of forward beating cilia runs between the right fold of the food groove and the exhalent pseudo-siphonal process on the right side of the cephalopedal complex. Along this tract, the tube of sperm can be seen to steadily extrude by thrust and ciliary action towards the aperture opening. At this time the head-foot is stretched forward and out of the aperture…" (Kennedy, 1995: 428). Kennedy also found that smaller males were proportionately more active than larger males in sperm transfer, and that about 15% of males and 3% of females were synchronously fertile at the maximum observed level of reproductive activity.

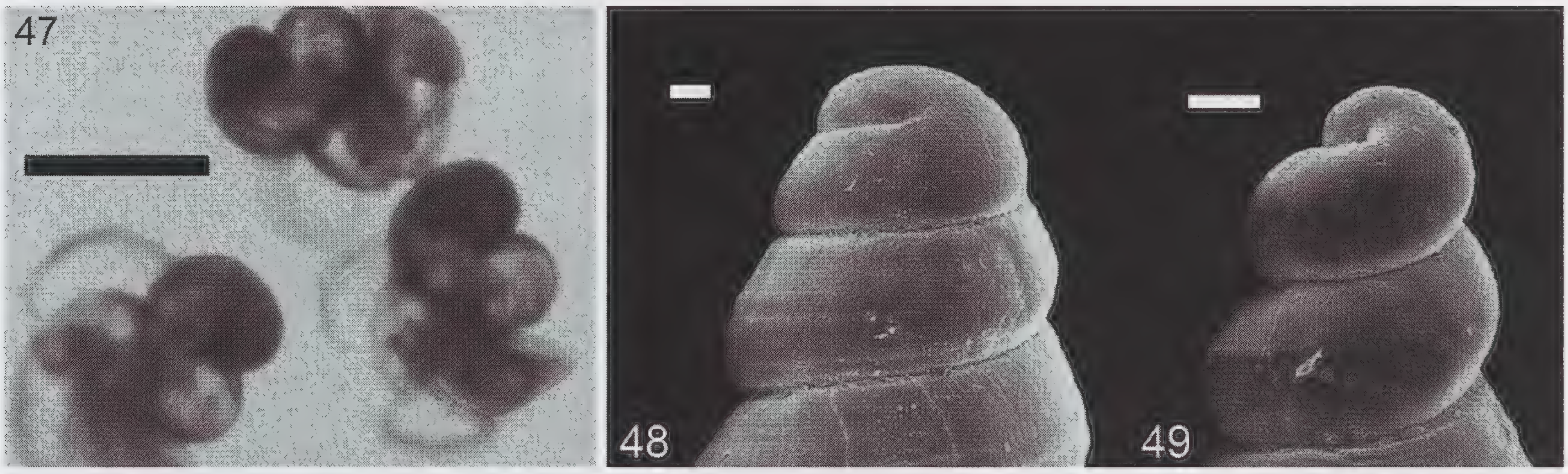
Fretter & Graham (1962: 361) suggested that in *Turritella communis*, "spawning of large numbers probably occurs simultaneously" (presumably meaning synchronous release of sperm by multiple males), but presented no definite evidence. In any case, several turritelline species certainly have "mass spawning" in the sense of many females laying eggs at one time: the confirmation by Kennedy (1995) of active aggregation of reproductive individuals of *T. communis* suggests that similar occurrences of high densities of similar-sized adults at times of reproduction in *T. gonostoma* Valenciennes, 1839, in the Gulf of California (Allmon, 1988; Allmon et al., 1992), *T. variegata* Linnaeus, 1758, in Venezuela (Bandel, 1975, 1976; Petuch, 1976), and *T. annulata* Kiener, 1843, in Ghana (Buchanan, 1958) may support similar interpretations. "Gregariousness," Kennedy concludes, "… appears to be a critically essential life strategy among these aphallic, internally fertilizing gastropods." (1995: 432) (see further discussion below). (As discussed by Gould & Robinson [1994: 371; following Hadfield & Hopper, 1980], because the common ancestor of all cerithioids was likely aphallate, this may have opened "evolutionary access to fertilization at a distance".)

Eggs and/or egg capsules have been described for six living turritelline species (*Turritella communis* [Lebour, 1933; Fretter & Graham, 1962; Kennedy & Keegan, 1992]; *T. variegata* [Flores & Macsotay, 1972; Bandel, 1975, 1976]; *T. gonostoma* [Allmon et al., 1992]; *T. cingulata* [Romero et al., 2003]; *Maoricolpus roseus* [Bax et al., 2003]; and *Vermicularia spirata* [Bieler & Hadfield, 1990]) (Figs. 43–46). In *T. communis*, the pallial duct ends in two pouches (Fretter & Graham, 1962; Figs. 2, 5); one serves as a receptaculum seminis, and sperm reach it through the mantle cavity by swimming against ciliary currents; the other pouch appears to be the location of fertilization of the eggs. After fertilization the eggs are packaged into capsules, consisting of up to 300 (for most species < 50) eggs embedded in albumen and surrounded by a wall which is secreted as the spawn mass passes out of the pallial duct. Hundreds to thousands of these capsules are then embedded in a mass of gelatinous matrix. The matrix is sticky, and the mass is usually covered with adhering sand grains or bound into a more fixed structure. The entire mass is usually unattached or only loosely attached to the substratum, and rolls along the bottom with currents. Development within the egg capsule lasts 7–18 days; generally the larger the egg size, the longer the intracapsular period (Romero et al., 2003). In both *M. roseus* and *V. spirata*, eggs are held by the female inside her mantle cavity until the planktonic larvae hatch (Probst & Crawford, 2008: 195; Bieler & Hadfield, 1990).

There is conflicting evidence of the existence of nurse eggs in turritellines. Pilkington (1974) concluded that in *Maoricolpus roseus*, although many eggs were laid per capsule,



FIGS. 43–46. Turritelline eggs. FIG. 43: Individual of *T. gonostoma* with eggs, northern Gulf of California. Shell length approximately 120 mm; FIG. 44: Diagram of egg capsules of *T. communis* attached to substrate (after Fretter and Graham, 1962). Scale bar = 2 mm; FIG. 45: *Maoricolpus roseus* w/eggs (from Bax et al., 2003; photograph by Felicity McEnnulty, CSIRO Marine and Atmospheric Research, Australia; reproduced with permission); FIG. 46: Egg string of V*ermicularia spirata* (from Bieler and Hadfield, 1990). Scale bar = 2 mm.



FIGS. 47–49. Larval and early adult whorls of living turritellines. FIG. 47: Light micrograph of veligers of *Turritella gonostoma* (from Allmon et al., 1992); FIG. 48: Scanning electron micrograph of the apex of an adult shell of *T. communis* from the English Channel, showing protoconch and protoconch-teleoconch boundary; FIG. 49: Scanning electron micrograph of the apex of an adult shell of *T. variegata* from Venezuela, showing protoconch and protoconch-teleoconch boundary. Specimens 48 and 49 in the collections of the Museum of Comparative Zoology, Dept. of Invertebrate Paleontology.

most embryos abort and serve as food for those that remain, and Peréz (1930) reported that leucocytes of *Turritella* are known to be phagocytic when engulfing their own unused ova. Similarly, Bax et al. (2003: 10) found that in *M. roseus* in Tasmania, "Up to 300 + very early stage embryos were observed within egg capsules in December, but only 50–100 veligers of 100–200 µm size in January, indicating number of embryos per capsule decreases as embryo size increases". In *M. roseus*, Probst & Crawford (2008: 195), however, reported "consistent observations of high numbers of veligers (up to 50) with highly synchronized development released from egg capsules", which would not be expected if nurse eggs were an important source of pre-hatching larval nutrition. *Vermicularia spirata* does not have nurse eggs (Bieler & Hadfield, 1990).

Reproduction appears to be more or less seasonal (late winter to early summer) in all living species that have been investigated. *Turritella gonostoma* in the northern Gulf of California deposits eggs in late winter and early spring (February–April) (Allmon, 1988; Allmon et al., 1992). Spawning females of *T. variegata* were collected on the Caribbean coast of Colombia in the winter (December–February) in two consecutive years (Bandel, 1976). *Turritella communis* spawns in the English Channel in the late spring (April–July) (Lebour, 1933; Wright, 1956; Fretter & Graham, 1962; Fretter & Manly, 1979; Kennedy, 1995). In *Maoricolpus roseus,* males have active sperm in the austral spring (September–October) and females have been observed to have egg capsules in spring and summer (September–February) (Pilkington, 1974; Bax et al., 2003). Carrick (1980a, b) observed oviposition by *Gazameda gunnii* in the austral summer (January), although the eggs are brooded in this species and metamorphosed juveniles are not released by the mother for another eight months (August). *Turritella cingulata* in Chile spawns in the austral spring and summer (September–March) (Romero et al., 2003).

Direct information on larval developmental pattern is available for seven living turritelline species (Table 2). Six of these have larvae that spend at least some time in the plankton, and one broods crawl-away larvae. In the species with pelagic larvae, the duration of their time in the plankton is relatively short (i.e., long-term planktotrophic – or teleplanic – larvae are not known). *Gazameda gunnii* from Australia is the only species known to have no planktonic larval period; it broods relatively large eggs within the mantle cavity for approximately 200 days, after which crawling juveniles are released (Peile, 1922; Iredale, 1924; Carrick, 1980a, b). The discovery of large numbers of tiny juvenile shells inside the shell of a conspecific adult has led to the inference of possibly similar ovoviviparity in at least six fossil turritelline species (Table 3). "Brooding" of a different sort occurs in at least one species: as described below, female *Maoricolpus roseus* hold their eggs within the mantle cavity for some time (Bax et al., 2003; Fig. 45) before the hatching of pelagic larvae.

Images and/or descriptions of veligers are available for at least five turritelline species: *Turritella gonostoma* (Allmon et al., 1992); *T. communis* (Fretter & Pilkington, 1970);

TABLE 2. Developmental patterns of larvae in living turritelline species.

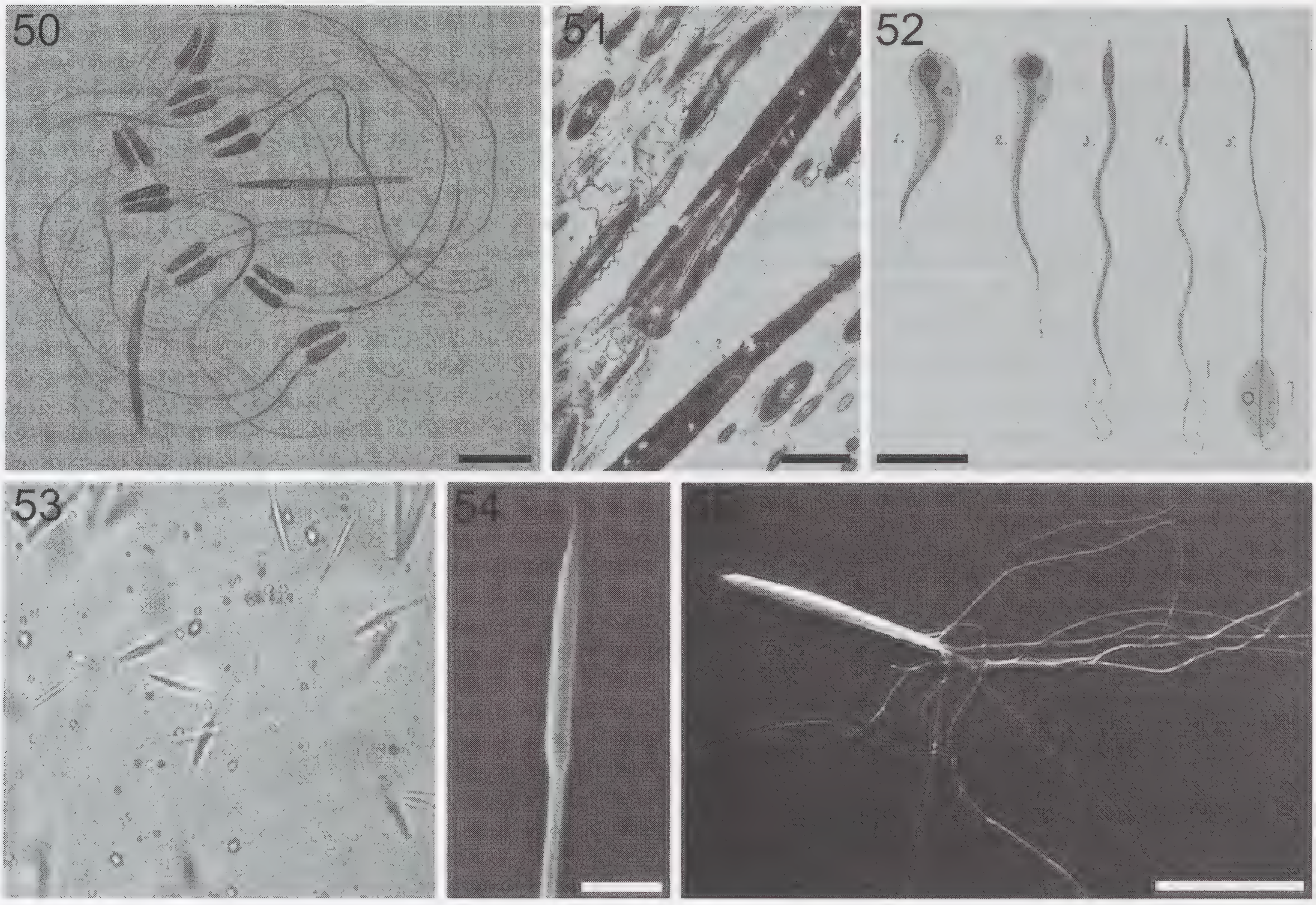
Species	Location	Planktonic phase duration (days)	Egg diameter	Reference
Turritella communis	NE Atlantic	14–21	100–139 µm	Lebour (1933); Kennedy & Keegan (1992)
Maoricolpus roseus	NZ, Australia	> 14	150 µm	Bax et al. (2003); Gunasekera et al. (2005); Probst & Crawford (2008)
Gazameda gunii	Australia	0	960–1000 µm	Carrick (1980a, b)
Turritella variegata	Venezuela	0–3	113 µm	Bandel (1976); Romero et al. (2003: 57)
Turritella gonostoma	Gulf of California	7–10	?	Allmon (1988); Allmon et al. (1992)
Turritella cingulata	Chile	?	92 µm	Romero et al. (2002, 2003)
Vermicularia spirata	Florida	?	300 µm	Bieler & Hadfield (1990)

Maoricolpus roseus (Bax et al., 2003; Gunasekera et al., 2005; Probst & Crawford, 2008); *T. cingulata* (Romero et al., 2003); and *Vermicularia spirata* (Bieler & Hadfield, 1990) (Fig. 47). Veligers of *M. roseus* have been maintained in laboratory aquaria for up to two weeks, where they were observed to feed on supplied microalgae (i.e., *Isochrysis*, *Pavlova*, *Nannochloropsis*, and *Caetoceros*) (Probst & Crawford, 2008: 193), and so should properly be termed "planktotrophic" (*sensu* Jablonski & Lutz, 1983). Apparently no direct observations of larval settlement and metamorphosis have been published.

Turritelline protoconchs consist of 2–5 smooth, rounded whorls, with the beginning of the teleoconch marked by gradual-to-abrupt appearance of one or more spiral ribs. The form of these protoconchs is generally consistent with Thorson's (1950) "apex theory" in reflecting developmental mode (Figs. 48, 49): planktotrophic species have relatively narrow, multispiral protoconchs, with the protoconch I (PI) usually clearly distinguishable from the larger protoconch II (P2); nonplanktotrophic species have larger, more rounded, paucispiral protoconchs, and the demarcation between PI and P2 is often faint or absent (Allmon, 1988; Bieler & Hadfield, 1990; see

TABLE 3. Instances of ovoviviparity in fossil turritellines reported in the literature.

Species	Age	Locality	Formation	No. of embryonic shells	Reference
Turritella alticostata	Miocene-Pliocene?	Rice's Pit, Hampton, Virginia	?	41	Antill (1974)
T. alumensis	Miocene	Alum Bluff, Florida	Choctawhatchee	48	Sutton (1935)
T. cumberlandia	Miocene	Plum Point, Maryland	Calvert	> 200	Burns (1899)
T. indenta	Miocene	Plum Point, Maryland	Calvert	"by the hundreds"	Burns (1899)
T. pilsbryi	Pliocene	Yorktown, Virignia	Yorktown	104	Palmer (1958)
T. pilsbryi	Pliocene	Yorktown, Virginia	Yorktown	47	Gardner (1948)
Zeacolpus taranakiensis	Pliocene?	Wellington, New Zealand	?	40-100	Marwick (1971a, b)



FIGS. 50–55. Sperm of three living turritelline species. FIG. 50: Cluster of paired adult euspermatozoa of *Turritella communis.* Scale bar ≈ 10 µm (from Bataillon, 1921); FIG. 51: Longitudinal section of the basal tract of a paraspermatic cell of *T. communis* (arrow indicates the insertion area of flagella; t = typical spermatozoa; g= granules). Scale bar ≈ 100 µm (from Melone et al., 1980); FIG. 52: Successive stages in the maturation of euspermatozoa of *T. communis.* Scale bar ≈ 400 µm (after Schitz, 1920); FIG. 53: Light micrograph of sperm of *Maoricolpus roseus* (from Bax et al., 2003); FIGS. 54, 55: Sperm of *Vermicularia spirata* (from Bieler and Hadfield, 1990). FIG. 54: Head of euspermatozoan. Scale bar = 2 µm; FIG. 55: Multiflagellate paraspermatozoan. Scale bar = 10 µm.

Jablonski & Lutz, 1983, for further discussion). Using this relationship, the developmental mode of a number of fossil turritelline species has been inferred (Jablonski, 1979; Dockery, 1993; Allmon, 1996; Bandel, 2006). Although some of these species have protoconchs indicative of long-term planktonic (planktotrophic) phases, most have protoconchs suggesting relatively short planktonic phases and so of relatively low dispersal potential (Allmon, 1996).

Spermatozoa

The sperm of most marine caenogastropods are of the "modified" type characteristic of species with internal fertilization (Franzén, 1955): each spermatozoan generally consists of three regions: an elongate pointed head, a long cylindrical middle piece, and a tail or flagellum (Franzén, 1955; Voltzow, 1994). Knowledge of turritelline sperm (Figs. 41, 42, 50–55) is based on data from five species: *Turritella communis* (Retzius, 1910; Bataillon, 1921; Franzén, 1955; Idelman, 1960; Melone et al., 1980; Afzelius & Dallai, 1983; Kennedy, 1995; Ishijima et al., 1999); *T. triplicata* (Schitz, 1920); *Maoricolpus roseus* (Bax et al., 2003); *T. cingulata* (Koike, 1985); and *Vermicularia spirata* (Bieler & Hadfield, 1990).

As in many caenogastropods, and especially cerithioideans (Healy & Jamieson, 1981; Healy, 1983, 1986), turritelline sperm are dimorphic: two distinct types of sperm are produced simultaneously within the male gonad of these two species. "Typical spermatozoa" (= "euspermatozoa") are capable of fertilization, and are also referred to as "eupyrene", meaning that they have nuclei containing the haploid number of chromosomes. "Atypical spermatozoa" (= "paraspermatozoa") are sterile, and can be "oligopyrene" (with only part of the haploid set) or "apyrene" (lacking nuclei altogether) (Fretter

& Graham, 1962: 338; Afzelius & Dallai, 1983; Kennedy, 1995; Ishijima et al., 1999; Pitnick et al., 2009) (Figs. 41, 42, 50–55).

The evolutionary significance of such sperm dimorphism (in gastropods as well as other groups) remains unclear, although numerous hypotheses have been proposed (Hodgson, 1997; Buckland-Nicks, 1998; Swallow & Wilkinson, 2002; Pitnick et al., 2009). The two most frequently mentioned are that paraspermatozoa serve as trophic resources (aka "provisioning" or "nurse cells") for euspermatozoa, and that they assist in transporting euspermatozoa to the ova for fertilization. Apparently neither of these hypotheses has been evaluated for cerithiacean gastropods.

In *Turritella communis*, the euspermatozoan (Fig. 42) is morphologically similar to those of other cerithioidean taxa (Franzén, 1955; Healy, 1983). The acrosome is elongated and conical, has a deep posterior invagination, and generally measures approximately 1.5 μm along its long axis; the even more elongated middle piece measures around 60 μm in length, and the free portion of the tail 40 μm (Afzelius & Dallai, 1983). The euspermatozoa of *T. communis* are often paired (Bataillon 1921; Franzen, 1955; Afzelius & Dallai, 1983) (Figs. 42, 50), as are those of *Vermicularia spirata* (Bieler & Hadfield, 1990) (Fig. 54), and can swim backward as well as forward (Afzelius & Dallai, 1983; Ishijima et al., 1999). Pairing of spermatozoa has also been described for three other animal groups (American marsupials, thrips, and dytiscid water beetles). The functional and adaptive significance of pairing are unclear, but have been assumed to enhance swimming ability and so ability to reach and penetrate the egg (Sivinski, 1979; Afzelius & Dallai, 1983), although the paired sperm do not swim faster than single sperm (Ishijima et al., 1999), in contrast to the situation in other animal groups (Pitnick et al., 2009: 104). In turritellines, the pairing occurs at the acrosome and nucleus, with the middle pieces and tail free and mobile (Idelman, 1960; Afzelius & Dallai, 1983).

The paraspermatozoan in *Turritella communis* (Melone et al., 1980; Figs. 50, 52) is also similar to those in other cerithioid species (Healy, 1986). It is composed of two parts: an elongate subconical "head" approximately 20 μm long and 1.5 μm in diameter, and a set of 8–9 flagella. The parasperatozoa of *Vermicularia spirata* are multiflagellate (Bieler & Hadfield, 1990; Fig. 54).

GROWTH

In at least two species (*Turritella communis* and *Maoricolpus roseus*), shell length is highly correlated to body mass (Thorson, 1965; Taylor, 1998; Fig. 56). If this pattern holds in the rest of the group, then shell size is a valid proxy for body mass in both living and fossil species, which would allow estimation of biomass from shell size alone.

Age of reproduction in living turritellines has not been determined by direct observation. Wright (1956) observed well-developed gonads in individuals of *Turritella communis* as small as 23 mm in length. According to the growth curves calculated by Cadée (1968), this corresponds to an age of less than one year. The life span of *T. communis* is unknown. Maximum reported size is approximately 45 mm; this corresponds to an age of just over two years on Cadée's curve. In contrast, J. B. Buchanan (pers. comm., 1987) attempted to age individuals of *T. communis* by counting collabral growth lines, and on this basis, suggested longevity of at least 15 years for this species, with population modes of 10–11 years. According to Carrick (1980a), reproduction in *Gazameda gunnii* begins when the adults are 2.5–3 years of age, and is repeated annually throughout a lifespan of 6–7 years.

Oxygen isotope sclerochronology (Jones, 1998) has been used to estimate age and growth rate for more than a dozen fossil and living turritelline species (Fig. 57). These data suggest that most species live to be no more than 3–5 years old and that growth is more rapid in juvenile stages. Two different studies of age and growth rates via isotopic analysis in living *Maoricolpus roseus* (Allmon et al., 1994; Scott, 1997) suggest that age and size of maturity in this species may vary between locations (Bax et al., 2003: 10). Scott (1997) found that shell growth was seasonal, with the most rapid growth during the warmest months, particularly during the first year of life, and that growth ceases at temperatures below 13°C and above 17°C.

Several authors have made circumstantial arguments for a positive correlation between abundance of potential food (phytoplankton) and turritelline shell size (Allmon et al., 1994; Teusch et al., 2002; Pietsch et al., 2007; Probst & Crawford, 2008), but this relationship has not been tested experimentally.

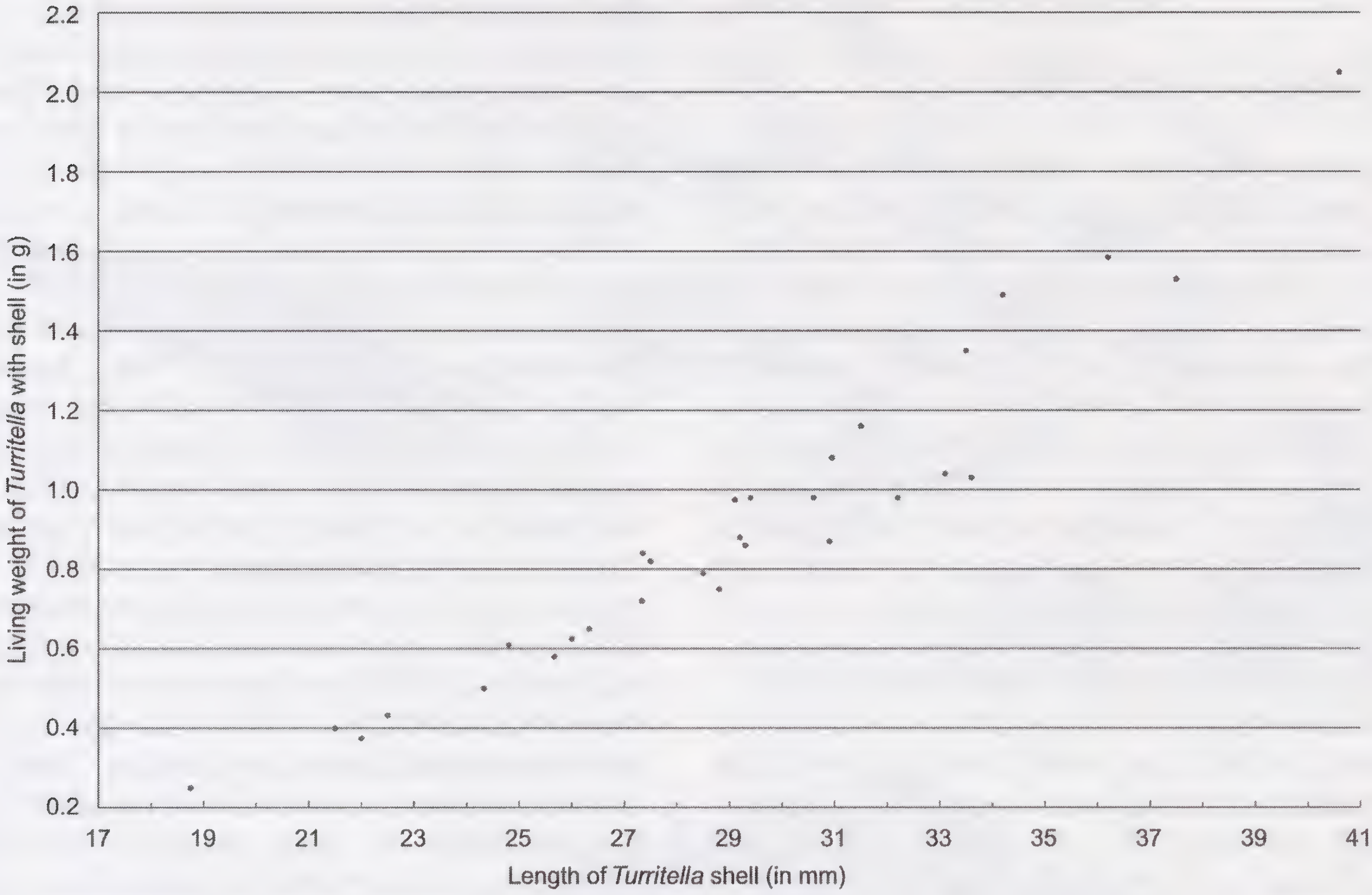


FIG. 56. Length to body weight of *T. communis* (from Thorson, 1965).

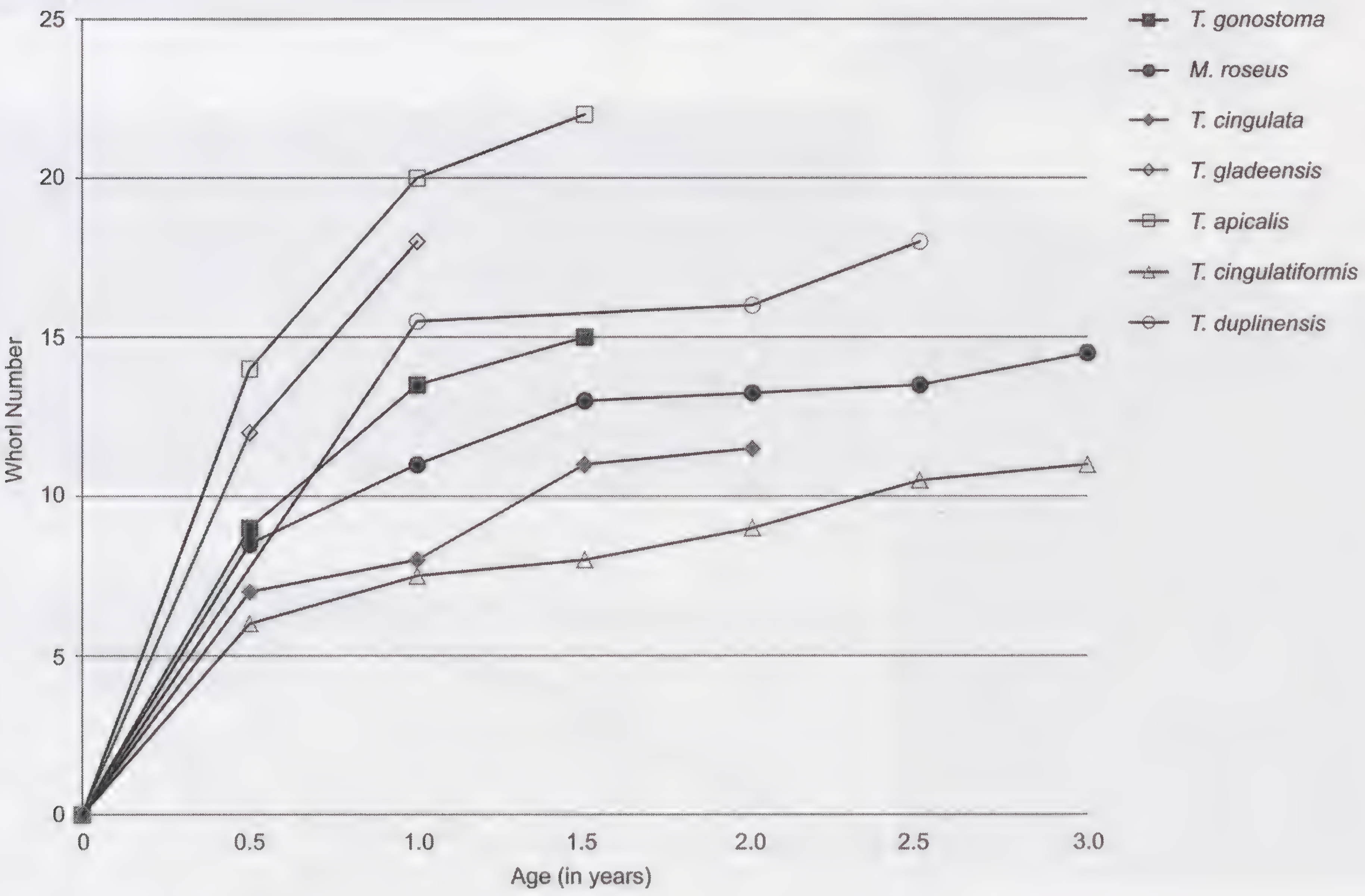


FIG. 57. Growth curves of fossil and Recent turritelline species, based on oxygen isotope sclerochronology. Data on *T. duplinensis* courtesy of Elizabeth Petsios. All other data from Jones (1998).

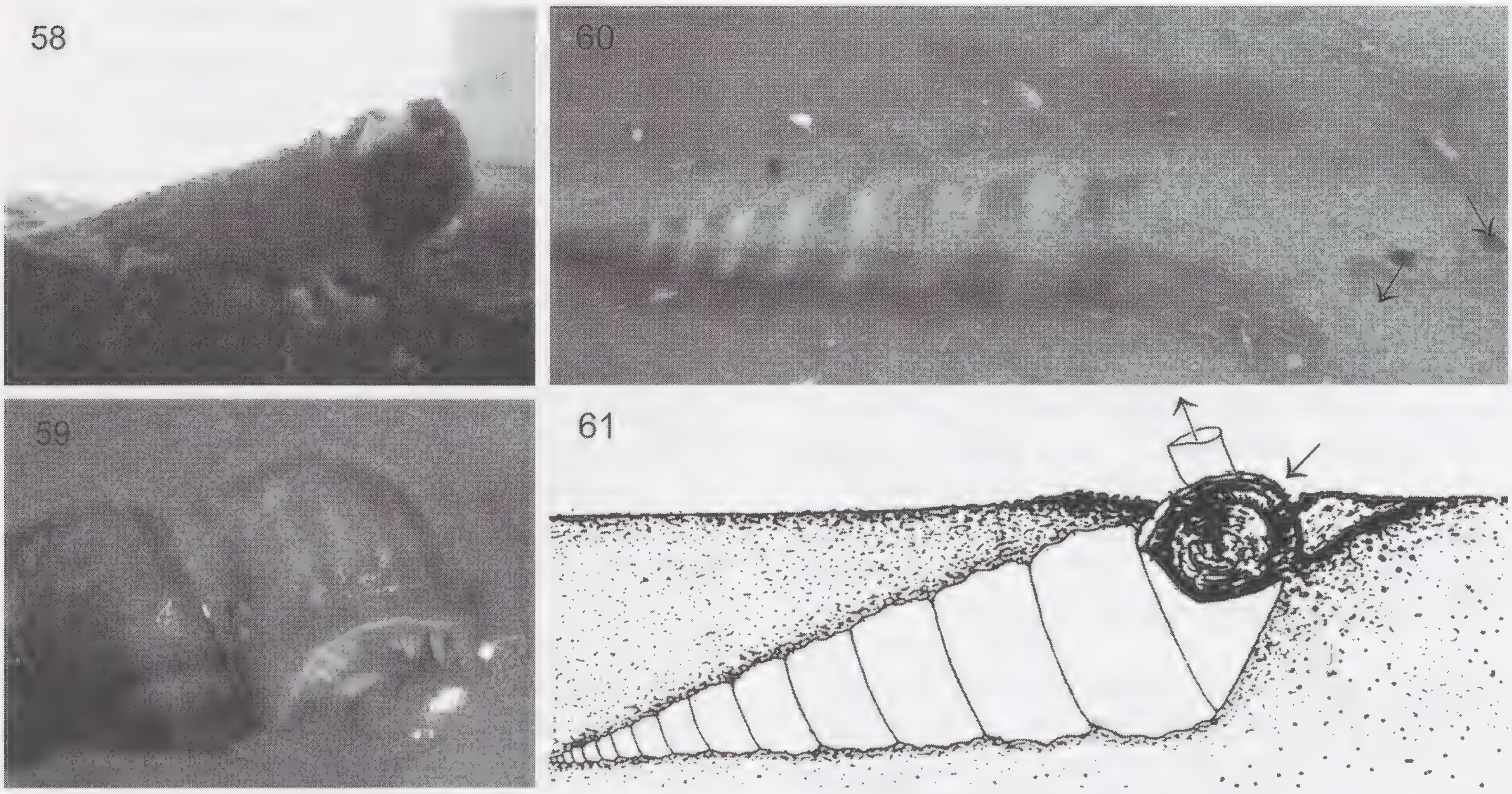
ECOLOGY

Life Position and Behavior

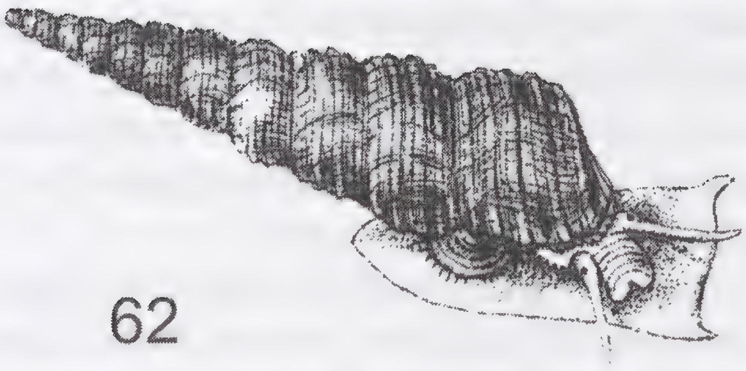
Healthy free-living adult turritellines most frequently assume two orientations on their usual substrata of soft mud or sand (Figs. 58–61). The first, assumed when at rest and suspension feeding, is with the long axis of the shell sub-parallel to the sediment surface and the aperture perpendicular to the substratum. The other, again with the long axis parallel to the sediment, but with the aperture facing the substratum, is assumed when the animal is crawling or burrowing. At least some species may regularly assume other orientations, for example when inhabiting more uneven (e.g., rocky) substrata (Allmon et al., 1994).

Some published illustrations have depicted turritellines with the animal crawling along the substratum with the shell elevated at approximately 45° (Figs. 62, 63), but this has apparently never been verified by reliable first-hand observation. The notion may have originated with Reeve (1860: 131), who wrote that: "The Turritellae [sic] are apparently a strong muscular group of mollusks, the disk being surmounted by a stout pedicle, by the strength of which the shell is borne up at an angle, but not allowed to trail upon the ground, as in the Cerithia [sic] and other elongated forms." The source of Reeve's comments is unclear, especially given that Kiener (1834) had already published a much more realistic illustration of a living turritelline, showing the shell being dragged along the substratum (Fig. 64).

Turritellines have long been thought to be essentially sedentary (Yonge, 1946; Marwick, 1957a; Bandel, 1976), and all living species for which observations have been recorded do indeed spend much of their time more or less stationary in their feeding orientation, either on top of or buried shallowly in the sediment. Because of this, they have a reputation of not being able to crawl long distances. Yet this inference may be unjustified, and movement may play a more important role in their ecology than has been recognized previously (Allmon, 1988). For example, patterns of seasonal appearance and disappearance of some species in particular areas, or of the absence of juveniles in many mass accumulations, may be due to movement over some distance (Wright, 1956; Allmon, 1988; Allmon et al., 1992; Chilcott, 1996, cited in Bax et al., 2003). Kennedy (1995) also demonstrated that *T. communis* "has a far greater



FIGS. 58–61. Normal feeding life orientation of living turritellines. FIG. 58: *Turritella banksi* from Panama, taken in aquarium; FIGS. 59, 60: *T. duplicata* from Thailand, taken in the field (courtesy of R. Waite). FIG. 59: View of body whorl of an individual buried in sediment, showing palial tentacles at edge of mantle cavity; FIG. 60: View of an entire buried individual, with arrows indicating direction of water flow into inhalant and out of exhalent openings; FIG. 61: Diagram showing pattern of water flow of an individual in this orientation, shallowly buried in sediment (modified from Healy & Wells, 1998).



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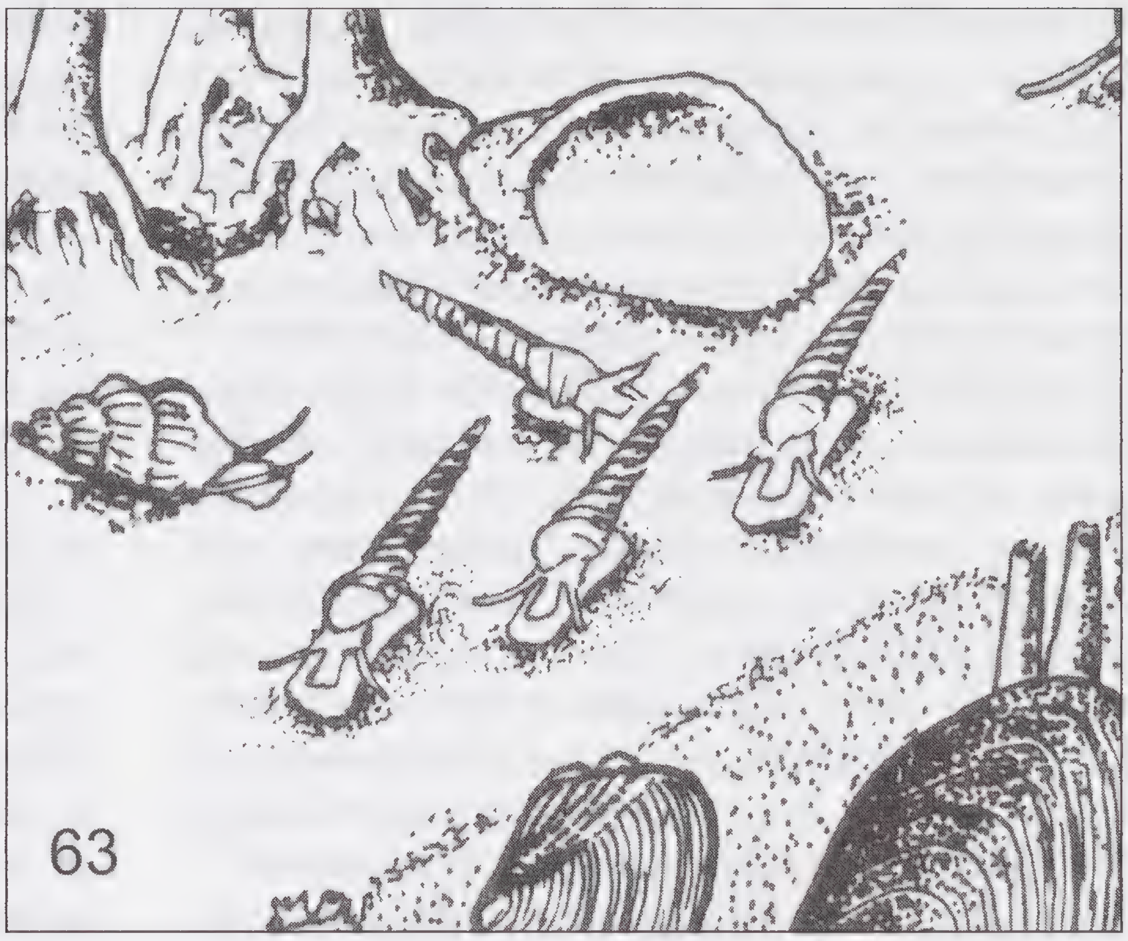

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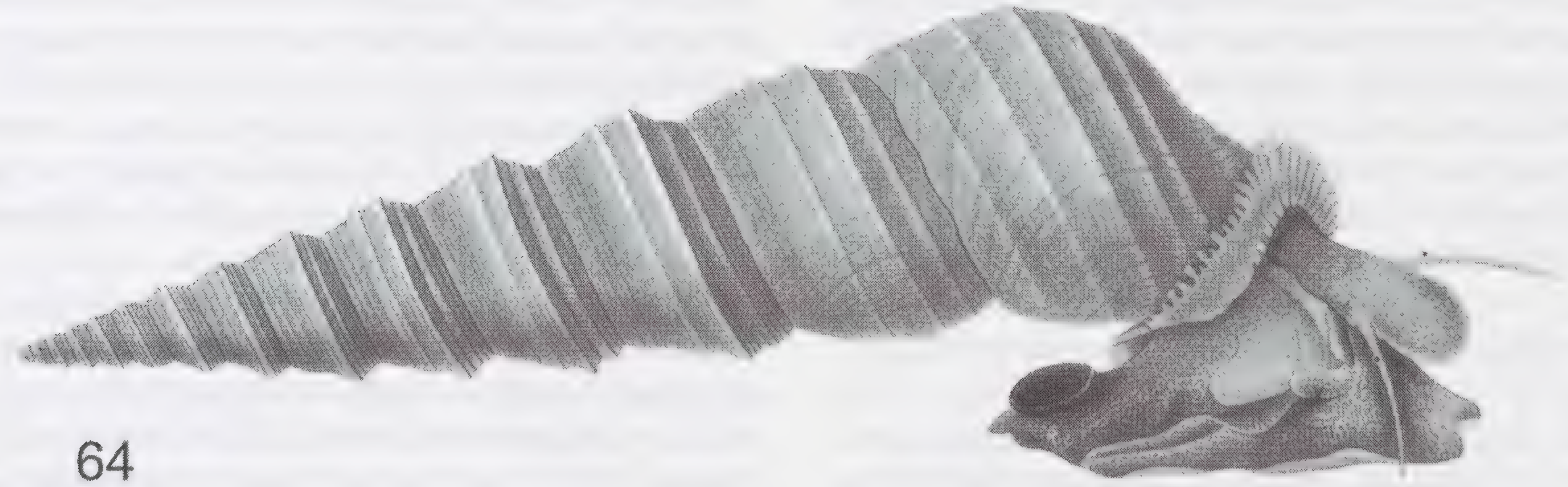

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FIGS. 62–64. Previous reconstructions of orientation of living turritellines while crawling on substrate surface. Figs. 62 and 63 are incorrect reconstructions showing the shell carried at an angle above the substrate, Fig. 64 is correct, showing the shell dragging on the substrate; FIG. 62 from Adams and Adams (1858), FIG. 63 from McKerrow (1978), FIG. 64 from Kiener (1843).

capacity for movement than was believed". Active crawling across the surface of soft substrata, leaving recognizable traces, has been documented in several living turritelline species (Allmon, 1988; Allmon et al., 1992; Kennedy, 1995; De, 1997, 2000; Allmon, unpublished observations; R. Waite, pers. comm.).

Burrowing behavior in turritellines has also been documented in a number of species (e.g., *Turritella communis* around the British Isles [Yonge, 1946; Kennedy, 1995]; *T. terebra* in Hong Kong [Hickman, 1983]; *T. variegata* in the southern Caribbean [Bandel, 1976; Petuch, 1976]; *T. gonostoma* in the Gulf of California [Allmon, 1988; Allmon et al., 1992]; *T. tricarinata* in the Mediterranean [Sartenaer, 1959]; *T. trisulcata* in the Red Sea [Allmon, 1988]; *T. banksi* in Panama [Allmon, unpublished observations]; *T. duplicata* in Thailand [R. Waite, pers. comm.]; and *M. roseus* in New Zealand and Australia [Allmon et al. 1994]. In all of these species, both crawling and burrowing is accomplished by first extending the foot over or into the sediment, and then pulling the rest of the body and shell forward in a series of abrupt but seemingly laborious heaves or jerks.

Although *Vermicularia*, with its uncoiled shell, is clearly modified for an almost completely sessile adult mode of life, even it can and does move (Gould, 1969; Hughes, 1985), extending its propodium forwards to grip the substratum, and then pulling the animal forward. Individuals have even been known to detach themselves from the substratum "by radular abrasion of the cement" (Hughes, 1985: 323). It is not clear when or why this occurs.

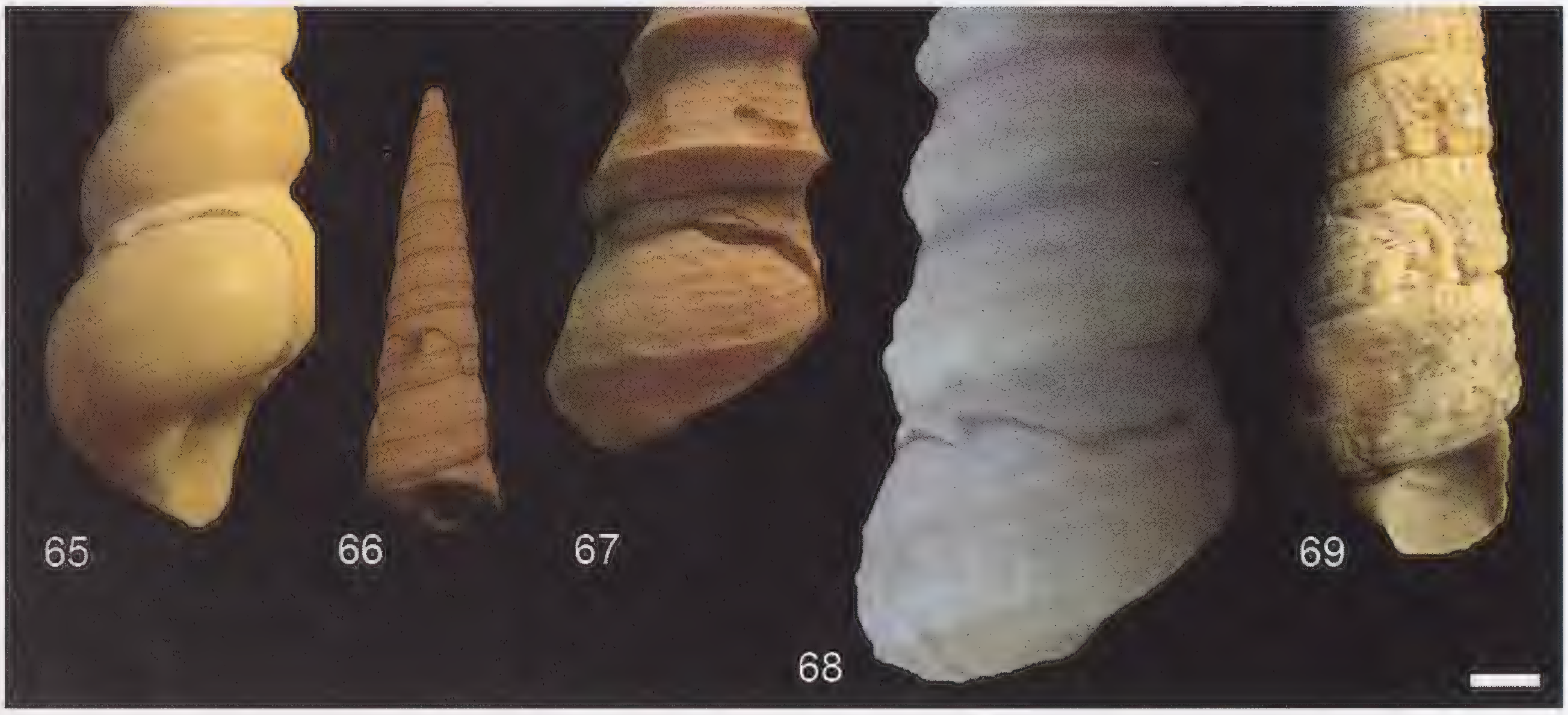
Bieler (2004) reported observing specimens of *Vermicularia* in the western Atlantic attached to a wide variety of substrata (e.g., sponges, hard coral, empty shells, rocks, algae, etc.). The occurrence of coiling in these instances, he suggested, may be the result of a balance between secure attachment and maintaining the aperture in a suitable position to feed from local currents (Bieler, 2004, and pers. comm., March 2011).

Several turritelline species have been observed in an almost vertical orientation, with the apex buried in the sediment and the aperture several centimeters above the sediment surface (Pinn, 1990; Allmon et al., 1992, 1994). Pinn (1990) reported "hundreds" of *Turritella duplicata* and *T. attenuata* in this orientation. He stated that "about half the shells stand upright at an angle of 90 degrees and the other half slanting at approximately 45 degrees". Pinn suggested that the snails do not attain this orientation by moving backward into the sediment, but by first digging down and then upward, after which they are exposed by tides or currents. Such behavior, however, has never been directly observed, and other observations suggest that such a posture may result from accidental orientation by currents (Allmon et al., 1994; R. Waite, pers. comm.).

Feeding

Although several early authors concluded that *Turritella communis* is a non-selective deposit feeder (Petersen, 1913; Hunt, 1925; Merriam, 1941), later studies showed that it is predominantly a ciliary suspension feeder (Graham, 1938; Yonge, 1946). As described above, food particles enter the mantle cavity where they are captured by the gill, and then transferred to the mouth via a mucus strand. Allmon et al. (1992) observed *T. gonostoma* in the laboratory and found that its feeding rates were much lower than expected compared to both other suspension feeding gastropods (e.g., *Crepidula*) and bivalves.

Yonge used observations of suspension feeding in *Turritella communis*, together with the generally reduced odontophore, radula, and salivary glands in this species, to generalize about the entire group, stating that "*Turritella* is an exclusively ciliary feeder" (1946: 379), and this was the prevailing view for the next half-century. Fretter (1975), however, pointed out that neither Graham nor Yonge made any observations on animals deprived of their normal food, when they might behave differently. A detailed study of the feeding behavior of the Australian turritelline *Gazameda gunnii* by Carrick (1980a) found that this species is not only a ciliary suspension feeder in the style of *T. communis,* but also a deposit feeder. *G. gunnii* apparently traps sediment with mucus strings extruded from the mantle cavity, and consumes these strings by means of its radula, much in the way that *T. communis* does the mucus that carries food particles out of its mantle cavity.



FIGS. 65–69. Breakage-and-repair scars in fossil and modern turritelline shells. FIG. 65: *Turritella cerea*, Recent, Darwin, Northern Territory, Australia, PRI Collection; FIG. 66: *Turritella* sp., Late Miocene, Darien, Panama, Natural History Museum Basel (NHMB) Collection; FIG. 67: *T. robusta*, Late Miocene, Darien, Panama, NHMB Collection; FIG. 68: *T. duplicata*, Recent, Penang, Malaysia, PRI Collection; FIG. 69: *T. variegata*, Recent, Venezuela, PRI Collection. Scale bar = 5 mm.

Analyses of gut and fecal contents show that *G. gunnii* consumes a range of material including diatoms, sponge spicules, bryozoan and crustacean skeletal fragments, and coarse siliceous sediment grains. *Gazameda gunnii* furthermore appears to partition its mode of feeding seasonally, according to local phytoplankton abundance, feeding on sediment when it is low, but acting as a ciliary suspension-feeder when it is high (Carrick 1980a).

In *Vermicularia*, feeding occurs in a similar way (Hughes, 1985; Figs. 7–11). The operculum protrudes from the shell and the head is approximately flush with the aperture. The sole of the metapodium faces upward, and the propodium is extended vertically with its sole facing forward. Pallial tentacles divide the entrance to the mantle cavity into a left incurrent and a right excurrent aperture. As in other species described above, particles in the incurrent stream are moved along the ctenidial filaments to the floor of the mantle cavity where they become bound in mucus, to a food groove to the right of the head, from the tip of which they are picked up by the radula and ingested.

Predators

Living turritellines are eaten by a wide variety of invertebrate and vertebrate predators (Table 4), including fish, turtles, seastars, crabs, and other gastropods. With few exceptions (Gaymer & Himmelman, 2008), however, living turritellines are occasional prey, and seem not to be especially heavily preyed upon by, or to be the principal prey of, any living predator.

Fish and turtles appear to consume turritellines by swallowing them whole or breaking them in their jaws and swallowing pieces (this is not always specified in the literature; Redon et al., 1994; Spring & Gwyther, 1999). Seastars evert their stomachs and envelope the apertural end of the shell, removing the soft parts and leaving little if any mark on the shell (Allmon et al., 1994). The exact means by which decapod crustaceans consume turritellines is not explicitly described in the literature, but at least some species swallow enough of the shell for it to be identifiable (Goñi et al., 2001; Fanelli & Cartes, 2004; Léon & Stotz, 2004).

Most fossil and recent turritelline shells show traces of breakage and repair (Figs. 65–69). Although some of this breakage is undoubtedly due to abiotic factors, resulting for example, from rolling of the shell by waves, many repaired breaks extend far behind the aperture, forming a deep repair scar of the type generally attributed to unsuccessful predation by decapod crustaceans that peel the shell back from the shell opening (Vermeij, 1982, 1983). Despite the widespread occurrence of such repair scars, however, there appear to be no published accounts of living decapods preying on turritellines by such peeling. As mentioned above, at least some turritelline species can retract into their shell more than 200° behind the unbroken aperture, the flexible and fringed operculum bending to allow withdrawal and simultaneous maintenance of water flow around it (Ankel, 1971; Fretter & Graham, 1981; Kilburn & Rippey, 1982: 52; pers. obs.); this is seemingly a useful defense against peeling predators.

There similarly appear to be no published accounts of direct observation of drilling predation on living turritellines, yet both fossil and recent turritelline shells frequently bear holes indicative of successful drilling predation (Dudley & Vermeij, 1978; Allmon et al., 1990). As is true for many other prey taxa, the identity of drilling predators on turritellines can be determined at least to some degree by the shape of the drillhole: naticid snails (family Naticidae) usually drill a beveled or parabolic hole, whereas muricid snails (family Muricidae) and octopus drill holes with relatively straight sides (Kitchell et al., 1981). Using this technique, a number of studies indicate that naticids are the most frequent drilling predators on fossil and living turritellines (Allmon et al., 1990; Tull & Böhning-Gaese, 1993; Hagadorn & Boyajian, 1997).

Other predatory gastropods attack turritellines through the aperture. In northern Venezuela, for example, *T. variegata* is preyed upon by at least five gastropod species, all of which apparently feed through the aperture of the snail (Petuch, 1976) (Table 4).

Parasites

At least four living turritelline species have been observed to be infected by trematode parasites (Platyhelminthes: Digenea) (Table 5), although these relationships have been studied in greatest detail in *Turritella communis* from the northeastern Atlantic. Trematodes are the most common metazoan parasites of gastropods (Poulin & Mouritsen, 2003). Like most trematodes, those infecting *T. communis* have a complex life cycle with three hosts (Kearn, 1998; Cribb et al., 2000): the first is the snail, the second a fish (usually a clupeoid or gadoid; Rothschild & Sproston, 1941; Wright, 1956; MacKenzie, 1985), and the third (the

TABLE 4. Predators of living turritelline species reported in the literature. References: 1 = Bax et al. (2003); 2 = Jones & Slinn (1956); Schafer (1972); 3 = Hunt (1925); Christensen (1970); 4 = Allmon et al. (1994); 5 = Petuch (1976); 6 = DuShane & Brennan (1969); 7 = K. Gowlett-Holmes (pers. comm.); 8 = Thorson (1965); 9 = Edgar (2000); 10 = Morton (1994); 11 = Spring & Gwyther (1999); 12 = Oliva & Carvajal (1984); 13 = León & Stotz (2004); 14 = Goñi et al. (2001); 15 = Redon et al. (1994); 16 = Ouannes-Ghorbel & Bouain (2006); 17 = Casale et al. (2008); 18 = Ortiz (2008); 19 = Davide et al. (2005); 20 = Fanelli & Cartes (2004); 21 = Gaymer & Himmelman (2008); 22 = Márquez (1990); 23 = Fehri-Bedoui et al. (2009); 24 = Matthews (1968); 25 = Paulay (2000); 26 = Albert (1995); 27 = Politou & Papaconstantinou (1994); 28 = Carpentieri et al. (2010); 29 = Nagabhushanam (1964); 30 = Fuentes (1981); 31 = Dodd (2009); 32 = King & Clark (1984); 33 = D. H. Graham (1939); 34 = Conway & Guinea (2011).

	Predator	Prey species	Location	Reference
Fish				
Elasmobranchii	Heterodontidae (horn sharks)			
	Heterodontus portusjacksoni	*M. roseus*	SE Australia	1
	Parascylliidae (collared carpet sharks)			
	Parascyllium ferrugineum	*M. roseus*	SE Australia	1
	Scyliorhinidae (cat sharks)			
	Asymbolus sp.	*M. roseus*	SE Australia	1
	Triakidae (hound sharks)			
	Mustelicus lenticulatus	*M. roseus*	New Zealand	4, 32
	Myliobatidae (eagle rays)			
	Myliobatis australis	*M. roseus*	SE Australia	1
	Urolophidae (round stingrays)			
	Urolophus cruciatus	*M. roseus*	SE Australia	1
Albuliformes	Albulidae (bonefishes)			
	Albula glossodonta	*T. cingulifer*	Tarawa	25
Batrachoidiformes	Batrachoididae (toadfish)			
	Amphichthys cryptocentrus	*T. exoleta*	Brazil	24
Scorpaeniformes	Triglidae (searobins)			
	Chelidonichthyes kumu	*M. roseus*	SE Australia	1
Perciformes	Citharidae (flounders)			
	Citharus lingulatus	*T. communis*	Mediterranean (Spain, Italy)	15, 27, 28
	Labridae (wrasses)			
	Notolabrus tetricus	*M. roseus*	SE Australia	1
	Pseudolabrus psittaculus	*M. roseus*	SE Australia	1
	Ophthalmolepis lineolatus	*M. roseus*	SE Australia	1
	Symphodus (Crenilabrus) tinca	*T.* sp. (probably *T. communis*)	Mediterranean (Tunisia)	16
	Semicossyphus maculatus	*T. cingulata*	Chile	30
	Gadidae (cods)			
	Gadus morhua	*T. communis*	North Sea (Kattegat)	2
	Gadus merlangus	*T. communis*	Irish Sea	29
	Melanogrammus aeglefinus	*T. communis*	Norway	26
	Trisopterus minimus	*T. communis*	Greece	27
	Moridae (morid cods)			
	Pseudophycis bachus	*M. roseus*	New Zealand	33

(continues)

(continued)

	Predator	Prey species	Location	Reference
	Haemulidae (grunts)			
	Anisotremus scapularis	*T.* sp. (probably *T. cingulata*)	Chile	12
	Uranoscopidae (stargazers)			
	Kathetostoma leave	*M. roseus*	SE Australia	1
	Callionymidae (dragonets)			
	Synchiropus calauropomus	*M. roseus*	SE Australia	1
	Pinguipedidae (sandperches)			
	Pinguipes chilensis	*T. cingulata*	Chile	18
	Cheilodactylidae (morwongs)			
	Cheilodactylus variegatus	*T. cingulata*	Chile	18
	Sparidae (porgies)			
	Pagellus acarne	*T. communis*	Mediterranean (Tunisia)	23
	Pagrus auratus	*M. roseus*	New Zealand	31
Tetraodontiformes	Monacanthidae (filefishes)			
	Parika scaber	*M. roseus*	SE Australia	1
	Meuschenia freycineti	*M. roseus*	SE Australia	1
	Diodontidae (porcupine fishes)			
	Diodon nichthemerus	*M. roseus*	SE Australia	1
	Allomycterus pillatus	*M. roseus*	SE Australia	1
Turtles				
	Lepidochelys olivacea	*T. terebra*	New Guinea	11
	Lepidochelys olivacea	*T.* sp.	Mexico	22
	Caretta caretta	*T. communis*	Mediterranean	17
	Caretta caretta	*T. terebra*	N. Australia	34
Decapods				
	Cancer polyodon	*T. cingulata*	Chile	13
	Palinurus elephas	*T.* sp. (probably *T. communis*)	NW Mediterranean	14
	Plesionika edwardsii	*T.* sp. (probably *T. communis*)	SW Mediterranean	20
Asteroids				
	Astropecten sp.	*M. roseus*	SE Australia	7
	Heliaster helianthus	*T. cingulata*	Chile	18, 21
	Luidia sp.	*M. roseus*	SE Australia	7
	Meyenaster gelatinosus	*T. cingulata*	Chile	18, 21
	Patitiella regularis	*M. roseus*	Tasmania	1
	spp.	*T. communis*	English Channel	3
	spp.	*T. anactor*	Gulf of California	6
	Uniophora spp.	*M. roseus*	Tasmania	1
Echinoids				
	Paracentrotus lividus	*T. communis*	Mediterranean (Croatia)	19

(continues)

(continued)

	Predator	Prey species	Location	Reference
Gastropods				
	Xymene ambiguus	*M. roseus*	New Zealand	4
	Scaphander lignarius	*T. communis*	Denmark	8
	Fasciolaria tulipa	*T. variegata*	Venezuela	5
	Melongena melongena	*T. variegata*	Venezuela	5
	Chicoreus brevifrons	*T. variegata*	Venezuela	5
	Voluta musica	*T. variegata*	Venezuela	5
	Phyllonotus globosus	*T. variegata*	Venezuela	5
	Pleuroploca australasiae	*M. roseus*	Tasmania	1, 9
	Rapana bezoar	*T. bacillum*	Hong Kong	10

primary or "definitive" host) a bird or fish. Most trematodes infecting marine gastropods have seabirds as definitive hosts (Wright, 1971). In the case of at least one species infecting *T. communis* (*Cercaria doricha* Rothschild, 1935), however, definitive hosts have been identified as including several fish species (*Lophius piscatorius* Linnaeus, 1758; *Scophthalmus maximus* Linnaeus, 1758; *Squatina squatina* Linnaeus, 1758; *Gadus pollachius* Linnaeus, 1758; *Raja* spp., *Trigla* spp.) (Fretter & Graham, 1962: 610).

In trematodes infecting marine gastropods, the eggs are released from the primary host via feces into the water, from which they are ingested by the snail (Wright, 1971). Within the snail, the parasite passes through three stages or generations (Cribb et al., 2000). First the eggs hatch into a free-swimming stage called a miracidum (which have been found in the stomach and intestine of *T. communis* [Wright, 1956]). The miracidia encyst in the snail's body wall in structures known as sporocysts, inside which the parasite replicates asexually, producing tiny embryos, known as redia. These then mature into a motile form called the cercaria which, after a period of at least 6–7 months (Wright, 1956: 32), emerge from the snail via the mantle cavity (Wright, 1956: 39). In *T. communis*, emergence occurs mainly during a period of about four months in spring and summer (Wright, 1956; MacKenzie, 1985). On emergence, the cercariae swim for a period of about two days (Ginetsinskaya, 1970) before being ingested by the second (intermediate) host fish (MacKenzie, 1985). In the fish, the parasites settle in the intestine, in which they develop into a encysted stage called a metacercaria, and where they can remain for 10 years or more (MacKenzie, 1985). When the intermediate fish host is eaten by the primary bird or fish host, the parasite reproduces sexually and lays eggs (Wright, 1971), and the cycle starts again.

Identification of species in Digenea is often difficult. The morphological differences between different species in the adult stage may be very small, but species can have widely different types of life cycles and morphologically distinct larvae (Wright, 1971). Knowledge of all of the different stages in these life cycles is very incomplete, and the cercaria stage is usually the best known (Cribb et al., 2000). This is the case for most of the forms observed to infect *Turritella communis*, most of which have been assigned only to the "genus *Cercaria*" (Table 5). At least three of these forms ("*C. rhodometopa*", "*C. doricha*", and "*C. pythionike*") are known to be larval stages of one or more species of the genus *Renicola* (Wright, 1953, 1956; Stunkard, 1964; MacKenzie, 1985) in the family Renicolidae. Renicolid trematodes are known to be parasites in the kidneys of birds and the family includes more than 50 species (Wright, 1971; Yamaguti, 1971; Munyer & Holloway, 1990).

The effects of trematode parasites on infected marine gastropods are poorly studied. Parasites are known to be important components of shallow marine ecosystems (Rohde, 1993; Mouritsen & Poulin, 2002; Poulin & Mouritsen, 2003; Thompson et al., 2005; Larsen & Mouritsen, 2009), and trematodes can cause major fitness reductions in their snail hosts (Poulin & Mouritsen, 2003). They have therefore been cited as potentially significant influences on marine gastropod evolution (Ruiz, 1991; Krist, 2001; Poulin & Mouritsen, 2003). The outcome of trematode infection in many mollusks is disappearance of the gonad (Laukner, 1980; Mouritsen & Poulin, 2002), and may also include decreased growth and increased mortality (Laukner, 1980; Huxham et al., 1993; Lafferty, 1993). The sporocysts of at least one trematode species, *Cercaria doricha*, are known to cause the disappearance of the gonad of *Turritella communis*, apparently by starving it of nourishment, but do not otherwise appear to harm the snail (Pérez, 1936; Negus, 1968). Bieler & Hadfield (1990:207) reported that 17% of 77 specimens of *Vermicularia spirata* they examined "were castrated by heavy trematode infections of the gonads". Pelseneer (1926) reported that trematode infestation affected sex ratio in *T. communis*. Trematode infection has been shown to cause changes in shell morphology in a variety of gastropods (Krist, 2000; Hay et al., 2005; Miura et al., 2006), although this has not been reported in turritellines.

Observed trematode infection rates of *Turritella communis* vary from 1–16% and have been described as "high" (Rothschild, 1935; Wright, 1956; Stunkard, 1964), but much higher rates (up to 97%) are known in many other marine gastropods (Poulin & Mouritsen, 2003), so it is not clear how important such infections are for turritellines. Rothschild (1935) and Wright (1956) reported that males are infected at much higher rates than females. The generally accepted explanation for this pattern is that the male gonad is active throughout the year and is therefore a more consistent host tissue for the parasite (Rothschild, 1935; Wright, 1956: 26).

TABLE 5. Parasites known to infect living turritellines.

Parasite higher taxon	Parasite species	Turritelline species	Notes	Reference
Gregarines (apicomplexan protists)	?	*T. communis*		Trégouboff (1918)
Trematodes (Platyhelminthes, Digenea)	*"Cercaria" rhodometopa*	*T. communis*	in gonads	Pérez (1924); Rothschild (1935); Hansson (1998)
	"Cercaria" pythionike	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" doricha	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" doricha-pigmentata	*T. communis*		Wright (1956)
	"Cercaria" nicarete	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" herpsyllis	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" turritellae	*T. communis*	in gonads and digestive gland	Hutton (1955); Hansson (1998)
	"Cercaria" ampelis	*T. communis*		Rothschild (1935)
	"Cercaria" ranzii	*T. communis*		Rothschild (1935)
	"Cercaria" cooki	*T. communis*		Wright (1956)
	Cercaria caribbea XVIII	*T. exoleta*		Martorelli et al. (2008)
	Cercaria melanocrucifera	*T. attenuata*		Reimer & Anantaraman (1968)
	Cercaria kuwaitae VII	*T. exoleta*		Abdul-Salam & Sreelatha (1996)
	unidentified	*Vermicularia spirata*	gonads	Bieler & Hadfield (1990)

Several species of pyramidellid gastropods have also been reported as parasitic on *Turritella communis* in the northeastern Atlantic (Table 5). Not all of these reports, however, may actually represent parasitism. As noted by Robertson & Mau-Lastovicka (1979), observations of associations in the field, and even animals in "feeding positions" in the lab, do not prove parasitism; feeding has to be seen and the parasite and host must be known to occur naturally in the same habitat. Smart (1887) reported "*Odostomia pallida*" (= *Brachystomia eulimoides* [Hanley, 1844]) "on the operculum" of *T. communis*; he did not mention feeding, but did note that the pyramidellids were withdrawn deeply into the shell with the operculum. Unaware of Smart's short paper (Ankel & Christensen, 1963:21), Ankel (1959) documented in detail parasitic feeding of "*Odostomia ambigua*" (= *Brachystomia eulimoides*) on *T. communis* in the laboratory, but the two can live in different habitats. Barnes (1994: 128) stated that *Brachystomia eulimoides* is "A common micro-predator of … *Turritella*…", presumably referring to parasitism, but he gave no reference or other information. Ankel (1959: 16–17) also observed *Brachystomia albella* on *T. communis* in the lab for 10 hours but he did not see it. Minichev (1971) observed "*Odostomia*" *fujitanii* actually feeding on *Turritella fortilirata* in the lab, but again the two species may not naturally co-occur in the same habitat. Køie (1989: 361) stated that in the western Kattegat off Denmark, "*O. eulimoides* parasitizes … *Turritella communis*", but it is not clear that this was based on any new observations.

Commensals and Epibionts

Living turritellines are known to host a large diversity and abundance of commensals and epibionts. The limpet *Capulus ungaricus* Linnaeus, 1758, for example, is commensal on *Turritella communis*, attaching to the shell inside the aperture of its living host, apparently without harming it (Thorson, 1965). Another patelliform gastropod, *Crucibulum quiriquinae* Lesson, 1830, attaches to the outside of the shells of living *T. cingulata* in Chile (Véliz et al., 2001). At least one species of hydroid, *Leuckartiara octona* Fleming, 1823, is found frequently on living and dead shells of *T. communis*, with two forms of the species occurring on different parts of the living snail (Rees, 1967). At least some of these hydroids capture emerging cercariae of the trematode *Renicola* (Wright, 1956: 38).

After the death of the snail, turritelline shells are frequently inhabited by hermit crabs (Paguridae) (Walker, 1992; Manjón-Cabeza & Raso, 1999; Barria et al., 2006), and other epibionts are frequently associated with these hermited (or "pagurized") shells. The cheilostome bryozoan *Hippoporidra senegambiensis* (Carter, 1882), for example, is frequently found on shells of *Turritella annulata* Kiener, which are inhabited by the pagurid *Diogenes ovatus* Miers, 1881 (Bassindale, 1961; Cook, 1964). The bryozoan *Lepralia edax* (Busk, 1859), which encrusts both gastropod and bivalve shells, dissolving the shell of the host and replacing it with its own construction (Hincks, 1880), has been reported on turritellines (Hyman, 1967: 381). Other hermit-associated epi- or endobionts on turritellines include bryozoans, corals, hydroids, spionid worms, sponges, and calcareous algae (Scott, 1885; Walker, 1992, 1998; van Soest, 1993). Empty turritelline shells may also be inhabited by other animals besides hermit crabs. The sipunculid *Phascolion strombi* (Montagu, 1804) frequently inhabits empty shells of *T. communis*, and is itself parasitized by the pyramidellid gastropod *Menestho diaphana* (Jeffreys, 1848) (Kristensen, 1970; Gibbs, 1978).

Abundance

Although they occur at various densities, high abundance or "gregarious habit" has long been cited as characteristic of turritellines, both in modern and fossil assemblages, and some occurrences of modern turritellines are among the most abundant reported for any large marine gastropod (Allmon, 1988; Table 6). The frequently high abundance of *Turritella communis* led Petersen (1913) to recognize it as a diagnostic component of benthic communities in waters off Denmark, and Petersen's work led Powell (1937) and Thorson (1957) to recognize "ecologically parallel" turritelline-dominated communities in New Zealand and Japan, respectively. Similar turritelline-dominated assemblages have been reported from the Mediterranean (Giacobbe & Mondello, 1994; Panetta et al., 2003).

High abundance of turritellines in fossil assemblages is so frequent that informal geological terms such as "Turritella-rock" (not to be confused with "Turritella agate"; see Allmon, 2009) are regularly used to describe them (Allmon, 1988, 2007). Allmon (2007: 513) defined a "turritelline-dominated assemblage" as "a macrofaunal assemblage in which turritelline gastropods (1) comprise either at least 20% of the total actual or estimated biomass or at least 20% of the macroscopic individuals in

TABLE 6. Reports of high density of living turritelline species (see also Allmon, 1988: table 2).

Species	Locality	Density/m2	Reference
Maoricolpus roseus	Tasmania	> 1500	Probst & Crawford (2008)
Zeacolpus pagoda	New Zealand	1000-3500	Hayward et al. (1981)
Turritella cingulata	Chile	4000	Gaymer & Himmelman (2008)

the assemblage, and (2) are at least twice as abundant as any other macroscopic species in the assemblage". The term "turritelline-rich assemblage" is used for an assemblage that does not fit these quantitative requirements but in which turritellines are still the most abundant species (Allmon, 2007).

As discussed above, in the geological record the facies distribution of abundant turritellines through time suggests that their pattern of modern environmental occurrence is not completely representative. Abundant turritellines do occur in carbonate rocks, but these occurrences are concentrated in the Cretaceous and Paleogene, whereas they occur in siliciclastic facies throughout the history of the group, Early Cretaceous to Recent. Turritellines have therefore clearly undergone evolutionary change in their range of environmental occurrence over time; specifically they have shifted the thermal and facies distribution of abundance since the early Paleogene (warm to cool, carbonate + clastic to almost exclusively clastic), even while they maintained their preference for high nutrient-flux conditions. This change in the group occurred between the Cretaceous/early Paleogene and later Paleogene/Neogene (see Allmon [2007] for further discussion).

The frequently high abundance of turritellines suggests that they may be an example of the "Allee effect" (Stephens et al., 1999; Courchamp et al., 2008; also known as "inverse density dependence" or, in fisheries science, "depensation"; Liermann & Hilborn, 2001), in which individuals of a species benefit from the presence of conspecifics. The phenomenon can be caused by the necessity of high density for reproduction, predator avoidance, or other critical function. Kennedy (1995) specifically suggested that high turritelline abundance might be an example of Allee effect, and Allmon (1992, 2001) suggested that dependence on high abundance might make turritellines especially vulnerable to fluctuations in primary productivity.

TAPHONOMY

Information from living turritellines leads to mixed recommendations for taphonomic interpretations of fossil turritelline assemblages. In situ modern turritelline populations consist, at least at high densities, of large numbers of both living and dead shells (Holme, 1950; Buchanan, 1958; Sartenaer, 1959; Petuch, 1976). Giacobbe & Mondello (1994) emphasized the difference between the large number of dead shells of *Turritella communis* and the small number of living shells and described a "*Turritella thanatofacies*" in the Mediterranean. Nicastro et al. (2009) found that, on the southeastern coast of Australia, dead shells of *Maoricolpus roseus* were well preserved but their density did not increase in surface sediments over time. Instead, periodic burial was "sufficiently frequent to prevent the accumulation of shells in biologically active surface sediments", and kept this invasive turritellid from having marked effect on the native benthic biota. Near Auckland, New Zealand, dead shells of *M. roseus* are also much more common on tidal flats than living individuals, and most dead shells are pagurized and encrusted with calcareous algae and other epibionts (W. Allmon and U. Smith, unpublished observations).

Obviously fragmented, bored, or current-worn shells have been interpreted as having been buried after a significant post-mortem time interval at the sediment surface (Schafer, 1972; Allmon et al., 1995), although biological processes, such as habitation by hermit crabs, may alter this relationship (Walker, 1998). Use of "life position" criteria is common in taphonomic studies of benthic marine invertebrates, but information from living turritellines makes assumptions about life position in fossil assemblages problematic. Walker (1998) examined epibionts encrusting the inner surfaces of the shells of Recent *Turritella gonostoma* in the northern Gulf of California. She noted that on these shells the distribution of epibionts could be used as indicators of life position. Shells that had been inhabited post-mortem by hermit crabs had similar endobionts in higher frequencies, with the addition of the characteristic spionid trace fossil *Helicotaphrichnus* (similar results were reported for shells of *T. terebra* in Indonesia by Lescinsky et al. [2002]). Empty shells also had extensive clionid sponge borings and were more likely to have drill holes from predatory gastropods. Thus, Walker (1998) concluded that endobiont infestation is not restricted to empty shells, nor is it necessarily a reliable guide for "time since death" for fossils.

CONCLUSIONS

This review of the natural history of turritelline gastropods highlights not only what we do know, but also what we do not. Details of soft anatomy have been described for a very small number of species, and we really have no idea about ranges of interspecific variation in most characters. Radulae in particular have been strangely neglected. Although we know a good deal about growth rates, we know virtually nothing about either the functional or developmental biology of the turritelline shell. We know the basic reproductive and larval biology of several species: most appear to have short-term planktonic (planktotrophic?) larvae, but at least one is a true brooder. At least one other employs spermatophores, but we are still guessing, however, about mode of fertilization and larval behavior in most species. We know nothing at all about larval settlement. We know very little about diet and rates of feeding in the wild. Although there is strong circumstantial evidence for occasional movement by individuals over distances of more than a few centimeters, we are almost totally ignorant of behavior in the wild. Although there is strong evidence for a positive correlation of abundance with available nutrients and/or primary productivity, this has not been examined quantitatively or experimentally. Although turritellines are clearly eaten by many predators, we know very little about their actual interactions with these predators in nature, which makes posing and testing hypotheses about the influence of predation on their evolution very difficult.

All biology begins with natural history; that is, with basic observations about organisms and how they interact with their environment. This is especially true of evolutionary biology. No amount of genetic sequencing will ever reveal where species live or how they behave or move or feed or mate or react to predators or competitors. We are largely ignorant of even the most basic natural history information for the vast majority of species. This means that no matter how much else we learn about them, we cannot adequately understand how they came to be as they are.

Compiling natural history information of the type presented here is now both easier and more difficult than ever before. It is easier to assemble already existing data from the literature via increasingly complete on-line resources and sophisticated search tools. It is more difficult in many cases, however, to make new observations because many organisms no longer live where and how they once did. Just as the "crisis in systematics" focuses on describing species before they become extinct, so the "crisis in natural history" must focus on recording what those species do in their biotic and abiotic environments before opportunities to observe them in nature are gone. Clearly much of this information should come from new field observations. Yet a great deal of valuable data is available in both unpublished observations and scattered throughout the existing literature. There is an enormous need to gather new data, to mine and organize old data, and to encourage students and amateur and professional colleagues to do the same.

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